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EFFECTS OF LOW TEMPERATURES ON THE BLACK HILLS BEETLE
(Dendroctonus ponderosae Hopkins)

By

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EFFECTS OF LOW TEMPERATURES ON THE BLACK HILLS BEETLE
(Dendroctonus ponderosae Hopkins)

INTRODUCTION

It has long been recognized that low winter temperature is an important factor limiting the distribution of certain species of insects and that the effective temperature of the growing season is not the only factor in determining the northern limits. Abnormally or unseasonably low temperatures are frequently fatal to a large proportion of the overwintering broods of some insects and prevent them from becoming serious pests. In some cases these cold periods have been one of nature's valuable checks to bark beetle increases and have brought outbreaks under control or checked the impetus of the epidemic. Hopkins (1899) recognized the fact that low temperatures, during the winter of 1893, may have been responsible for the great reduction in the epidemic of the southern pine beetle (Dendroctonus frontalis Zimm.). Beal (1933), referring to the same insect, states that all past outbreaks have occurred in North Carolina following mild winters and that many severe outbreaks have been terminated by cold winters. Miller (1933) found that a cold spell during December 1932 killed 65 percent of the brood of the western pine beetle (Dendroctonus brevicornis Lec.) near Hackamore, Calif., and as a result it was possible to close a camp that was doing artificial control. Three cold periods during December 1932, February 1933, and November 1933 caused considerable

western pine beetle mortality in California, Oregon, and Washington (Koen and Furniss 1937). Two records of winter kill of the Black Hills beetle (Dendroctonus ponderosae Hopk.) have been made and others undoubtedly have occurred but have never been observed. In November 1932 an unseasonably low temperature killed 28 percent of the brood on the Pike National Forest and during the winter of 1932-33 L. G. Baumhofer, in an unpublished office memorandum of the Bureau of Entomology, United States Department of Agriculture, estimated a 50 percent mortality on the Roosevelt National Forest. Both of these forests are on the eastern slopes of the Rocky Mountains in the ponderosa pine type.

The Black Hills beetle is one of the most important forest insects in the United States and is undoubtedly the most serious enemy of pines throughout the central Rocky Mountain region. It has been responsible for the destruction of more merchantable timber in that region than has any other agency. It kills healthy, vigorous pines of practically all ages and species that occur within its range.

The present investigations were undertaken to determine the effect of low winter temperatures upon the Black Hills beetle and its relation to the occurrence of serious epidemics. Since epidemics of this insect occur at irregular intervals it was conceivable that the occurrence of fatal low temperatures might be one of the factors

responsible for the decline of the infestations. One of the chief aims of the economic entomologist is to foresee and prevent outbreaks. In order to do this, all environmental factors accompanying and causing outbreaks must be studied. Temperature is one of the factors of the environment, from which the insect cannot escape, and one which must be understood to devise means of control and prevention of damage.

LIFE HISTORY OF BLACK HILLS BEETLE

The life history and habits of this insect have been covered in a number of published articles by Hopkins (1902, 1905, and 1909), Blackman (1931) and Beal (1939) but will be reviewed briefly as an introduction to the studies that follow.

The Black Hills beetle occurs in pine-forested areas of southeastern Montana, western South Dakota, eastern half of Wyoming, and through Colorado, Utah, New Mexico, Arizona, southern California, and parts of Mexico (Figure 1). It attacks ponderosa, limber, lodgepole, whitebark, piñon, Mexican white, and bristlecone pines. The first four hosts mentioned are the most frequently attacked.

When the Black Hills beetle is not numerous it breeds in weakened or injured trees. Under favorable conditions it increases very rapidly and small centers of infestations increase rapidly in number and size, coalescing to form larger groups and causing



Figure 1. Distribution of the Black Hills beetle in the United States (after Hopkins). The weather stations from which minimum temperature records were taken are represented by crosses and the localities from which infested logs were obtained by small circles.

extensive losses. These epidemics continue until natural factors or artificial control terminate them.

Damage to the living tree is caused by the adults and larvae that work in the phloem. The peak of the flight is in August when the adults emerge and attack new green trees. The beetles construct long vertical galleries in the phloem parallel with the grain of the wood. They carry in a bluestaining fungus which permeates the wood, stopping sap conduction. Eggs are laid in niches along the sides of the egg gallery as it is being constructed. The eggs hatch in about 10 days and most of the larvae are at least half grown before winter. The larvae make feeding galleries more or less at right angles to the egg galleries. As the larvae grow the galleries become wider. The larvae resume feeding in the spring and during the latter part of May and the first part of June the larvae transform to pupae in cells in the phloem at the end of the larval galleries. The pupae transform into beetles during June. The adults remain in the inner bark feeding and do not emerge until August. Thus a generation is completed in one year at low elevations. At elevations between 9,000 and 10,000 feet, in the northern limits of the beetle's range, some of the brood require two years to complete the cycle.

DISCUSSION OF LITERATURE

The literature on the freezing process and cold-resistance of insects is now quite extensive. The most comprehensive early work on the subject was by Bachmetjew (1901). He summarized the work that had been done up to that time, performed numerous experiments, and drew conclusions regarding cold-resistance of insects. The more recent comprehensive publications on the theories and concepts of freezing and survival of insects are by Uvarov (1931), Payne (1926-28) and Salt (1936). There are now some very good economic papers on the practical application of low temperatures. Some of the best papers on the subject in addition to those mentioned above are by Back and Cotton (1924), Barber (1924), Batchelder and Questel (1933), Beal (1927, 1933), Carter (1925), Decker and Andre (1936), Fox (1936), Hodson (1937), Keen and Furniss (1937), Kozhantshikov (1938), Mail (1930, 1932), Mail and Salt (1933), Miller (1931, 1933), Nagel and Shepard (1934), Newcomer (1920), Payne (1926-1929), Robinson (1926, 1927, 1928), Sacharov (1930), and Sanderson (1908).

The cause of death from low temperatures has been considered as due to: (1) mechanical injury by formation of ice crystals in the cells; (2) dehydration of the cells through the freezing out of the water; and (3) precipitation of the proteins and the formation of irreversible chemical reactions. The first theory

has now been abandoned because of the failure of a number of workers to find any histological evidence in favor of it. The second theory, that the freezing of the water leaves the unfrozen parts more concentrated and thus toxic, still has support. The third theory is the most recent and also embodies some of the first two theories mentioned. It is held that a high degree of water crystallization causes dehydration of proteins, denaturation, and death of the organism.

It was first pointed out by Gueyland and Portier (1916) and later by Knight (1922) that there is a seasonal variation in the cold-hardiness of insects. Payne (1926) found that there is a marked correlation between the environmental temperatures and the insect freezing and undercooling points. This author studied three ecological groups: (1) oak borers, a group normally exposed to temperature extremes; (2) stored products insects; and (3) aquatic insects. Stored products insects and aquatic insects showed no periodicity but oak borers increased their cold-hardiness in the fall and lost this hardiness in the spring. In such insects as the oak borers, there exists in the winter time a secondary freezing point below that ordinarily found during the summer condition. The oak borers die at the first freezing point in summer condition and in a fully hardened condition die at the secondary freezing point. Payne also found

that the freezing points vary directly with the moisture content of the insect and that hardness could be increased by dehydration. The work of Robinson (1927, 1928), with several insects unequally resistant to cold, proved that in the resistant species the amount of free water decreased considerably and that the bound water increased when the insect was conditioned at low temperatures. The bound water is described as being absorbed by minute colloidal particles and will not freeze at temperatures above -20° C. Sacharov (1928, 1930), pointed out that there is a relation of hardness to the fat-water ratio. He found that the fat content in the hardy species was higher than that in the non-resistant ones. Kozhantshikov (1938) proposes a theory of cold-hardiness based on the type of cellular respiration the insect carries on. In non-hardy insects or during growing phases of hardy insects the cellular respiration is caused by oxydases, that act in connection with the structural elements of the cells. The crystallisation of the water in the cells stops respiration and causes death. In cold hardy insects, which are able to withstand freezing, the cellular respiration is carried on by dehydrases. Cellular respiration of this type does not depend on the structural elements of the cells but is probably connected with non-saturated fats. Since freezing of the protoplasmic water does not affect respiration caused by the action of dehydrases, the insect is

able to survive freezing.

The lethal effects of low temperatures on Dendroctonus were first noticed by Hopkins (1899) who concluded that the cessation of the epidemic of D. frontalis during the winter of 1893 was due to low temperatures and to one or more contagious diseases. In a later study Deal (1927, 1933) found low temperatures to be the most important limiting factor of the southern pine beetle. High brood mortality begins somewhere between $10^{\circ}\frac{1}{2}$ and 15° . Air temperatures as low as -5° destroyed all of the larvae, pupae, and adults except for a few specimens in well protected places. Field temperatures of -5° did not appear to affect the eggs. In one field test 43 percent of the larvae were killed at 10° , but all of this mortality occurred among the brood in the phloem where the moisture content is higher than in the outer bark.

The lethal low temperatures of the western pine beetle were determined by Miller (1931). The mortality of larvae at -5° exceeds 60 percent, and practically no larvae survive -10° . High mortality of the pupae occurs at temperatures between 5° and -5° and is complete at -8° . High mortality of the adults occurs between 12° and 5° and is complete at 0° . The eggs are more resistant, as 10 percent survived temperatures of -15° . The larvae freeze between

1. All temperatures are in the Fahrenheit scale unless otherwise indicated.

10° and 15°, but recover when raised to active temperatures again.

The effects of low temperatures on the western pine beetle were investigated in the field by Kean and Furniss (1937) following three periods of cold weather. In general, mortality varied inversely with the thickness of the bark. The mortality of the larvae in the moist inner bark was greater than that of the larvae a short distance from the phloem in the dry outer bark. Long cold periods were more effective than the short cold periods because of the lag of subcortical temperatures behind that of air temperatures. The lethal effects of low temperatures are evident in the infestation trends at a frequency of about once in every 10 years. Anything less than 50 percent reduction has little or no effect upon the annual infestation; therefore, this amount of kill or more is necessary to cause alteration in control work.

DESCRIPTION OF APPARATUS AND METHODS

Low Temperature Cabinet and Controls

The experiments were carried out in an automatically controlled well-type, low temperature cabinet designed by the Forest Insect Laboratory at Berkeley, Calif. and installed at Fort Collins, Colo., during the summer of 1936. The original control system was unsatisfactory and a new recording resistance thermometer controller was installed during January 1938. All temperatures were recorded in the Fahrenheit scale. The range of the cabinet was from 40° to -40°. A blower, inside of the cabinet, insured proper circulation and prevented air stratification.

Source of Larvae for Tests During the Season of 1936-37

Trees infested with the Black Hills beetle were cut into 40-inch lengths during the fall and hauled to a central storage at Allenspark, Colo. in the mountains west of Fort Collins where they were accessible for tests during the remainder of the winter season.

Infested ponderosa pine was obtained on November 2 and 3 at an elevation of approximately 8,000 feet from Deer Ridge near Allenspark, Colo. Several tests were made with grubs collected in the field during a control operation.

The limber pine larvae were obtained from trees cut on Boulder Ridge on the Roosevelt National Forest on November 4 at an elevation of 8,500 feet. The supply of limber pine larvae was exhausted before the spring tests were made. Two tests were made with larvae collected in the field near Allenspark, Colo.

Infested lodgepole pine was obtained on November 18 at an elevation of approximately 8,800 feet from Mullison Creek on the Medicine Bow National Forest. The material was packed out in slabs and covered with hot paraffin wax to prevent drying out.

Source of Larvae for Tests During the Season of 1937-38

Trees infested with the Black Hills beetle were cut into 40-inch lengths in the fall and taken to Redfeather Lakes, Colo. for storage.

Infested ponderosa pine was obtained on October 20 and 30 at an elevation of 7,500 feet from Big Elk Park on the Roosevelt National Forest.

Infested limber pine was obtained on October 25 at an elevation of approximately 8,500 feet from Pingree Park on the Roosevelt National Forest.

Infested lodgepole pine was obtained on October 29 at an elevation of approximately 8,500 feet from Lincoln Park on the Medicine Bow National Forest.

Source of Larvae for Tests During the Season of 1938-39

Infested material was cut in the fall and stored at Redfeather Lakes.

Infested ponderosa pine was obtained on October 17 and 18 at an elevation of approximately 7,500 feet from North St. Vrain Canyon on the Roosevelt National Forest.

Infested limber and lodgepole pine were obtained on October 19 and 20 from a control operation near the Cold Springs Ranger Station on the La Prele Unit of the Medicine Bow National Forest.

Source of Larvae for Tests During the Season of 1939-40

Infested sections were cut in the fall and stored at Redfeather Lakes as in the previous two seasons.

Infested ponderosa pine was obtained on October 12 from the

same vicinity as the previous season.

Infested limber and lodgepole pine was obtained on October 20 from the same vicinity as the previous season.

Storage of Infested Logs

Infested logs of each of the three hosts were stored at a central locality so that all would be subjected to the same conditioning temperatures and also be accessible by auto throughout the winter. The logs were stored in a shed at Allenspark, Colo., during the winter of 1966-67. During the following three winters the logs were stored at Redfeather Lakes, Colo., at an elevation of approximately 8,500 feet. The shelters were quite roughly constructed so as to allow free circulation of the air and yet protect the infested logs from the snow and rain (Figure 2). The storage locations were in the upper elevation range of ponderosa pine and the lower range for limber and lodgepole pine. A thermograph and maximum and minimum recording thermometers were set up under the shelters to record the conditioning temperatures.

Removal of Larvae from Logs

Before each test, infested logs were brought to Fort Collins, and the larvae removed from the bark in a room at approximately 65°. Most of the larvae from the three hosts were from one-half to three-quarters grown, although a few were nearly full grown and a few



Figure 2. Shelter at Redfeather Lakes, Colo., where the infested logs were stored in the fall for tests during the winter and spring. The thermograph and recording thermometers were operated in the box on top of the logs.

were less than half grown. An attempt was made to use larvae of a standard size, one-half to three-quarters grown, although this was not always possible. The larvae were placed in ointment tins with 50 paraffin cells with one larva in each cell (Figure 3) and stored immediately in a refrigerator at 32° to 35°. After a sufficient number of larvae were secured, they were dumped into a petri dish and mixed. The petri dish was immediately placed in an ice bath so that the larvae would not be exposed to developmental temperatures longer than necessary. After the larvae were mixed they were transferred to petri dishes with a layer of paraffin wax in the bottom of each, and into each of which 50 holes had been drilled with a twist drill (Figure 4). Each dish provided a sample of 50 larvae for exposure. All injured larvae were discarded and the petri dishes containing larvae were placed at 32° until tested. The larvae were handled with a small pair of forceps which were altered so that the points could not be forced shut and injure the larvae. A drop of solder was spotted on one of the jaws of the forceps about one-half inch from the point. The spot of solder was then filed down until it allowed the jaws of the forceps to come close enough together to hold the larvae but not injure them.

Exposure of Larvae

Exposures were made with larvae removed from the bark instead of exposing infested logs so as to eliminate such variables as bark thickness and moisture content. If logs were used much time

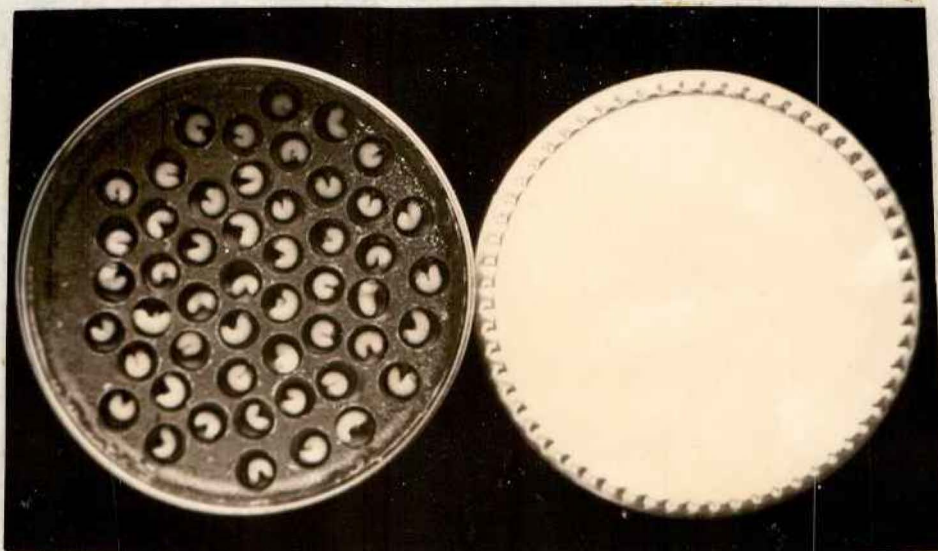


Figure 3. Ointment tin used to store the larvae after they are removed from the bark. Approximately natural size.



Figure 4. Petri dish with paraffin cells filled with larvae ready for exposure.

would be lost in reaching the desired temperature beneath the bark because of the lag of subcortical temperatures behind air temperatures.

In general, low temperature work with insects has been carried on in two different ways: First, by exposure of a fairly large number of insects at one time to a constant low temperature with varying time factors; and second, by exposure of individuals in contact with a thermocouple, which records the body temperature. The first method was applied to the Black Hills beetle.

The insects were exposed for 2 hours and 15 minutes, in lots of 50 or 100 in the petri dishes (Figure 4). The cabinet was held at a constant temperature and exposures were made in most experiments at $2\frac{1}{2}^{\circ}$ intervals. Most of the tests were started at or below the ultimate critical point (highest temperature at which 100 percent mortality results) and each succeeding test run at each $2\frac{1}{2}^{\circ}$ interval higher. After exposure, the frozen larvae are frosty-white and solid, while the unfrozen ones are cream colored. Mortality counts were taken at 24 hour intervals for 2 or 3 days after removal of the insects from the cabinet, and the count showing the greatest number of living insects was used in interpreting the results. During the course of the work a total of approximately 65,000 larvae were used.

RESULTS OF EXPERIMENTS

Determination of Survival after Exposure

During the fall and spring before and after the larvae have

reached their maximum cold-hardiness it is relatively easy to differentiate between living and dead grubs. The living grubs wiggle vigorously when observed at room temperature and the dead turn dark within a couple of days. From approximately December 1 to March 21 the larvae are more dormant and frequently show no signs of movement when left at 70° for several hours. During this period of maximum cold-hardiness and dormancy the larvae are straight and flattened dorso-ventrally as contrasted with the typical active larvae that are U-shaped and circular in cross section (Figure 5). These maximum cold-hardened larvae, that froze solid when exposed to low temperatures, showed signs of life after several days of exposure to room temperature. Although these frozen larvae were living some of them were not normal in their activity. Accurate mortality counts obviously could not be made because it was not known whether the injured larvae would recover and resume development.

In the tests made on February 4 and 5, 1937, duplicate samples, 50 each, of ponderosa pine larvae were exposed at the various temperatures and half of the samples placed in a refrigerator at 35° for 4 weeks, after exposure, before mortality counts were made. It was thought that by leaving the larvae in the refrigerator for 4 weeks the ones killed by the cold would be decomposed sufficiently to distinguish them from the living unfrozen ones, and that the supposedly dormant ones would show more activity. The results of this test are presented

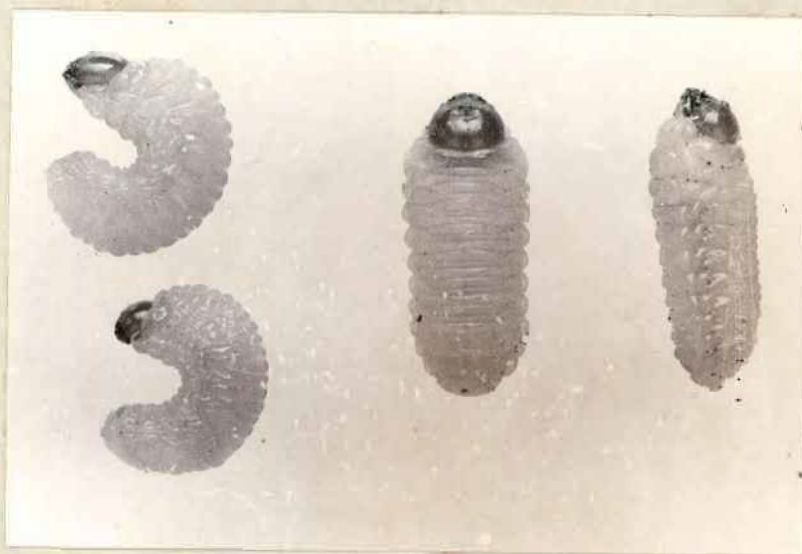


Figure 5. Larvae of Black Hills beetle, approximately 6 x. A, lateral view of two typical active larvae. B, Dorsal and lateral views of two dormant larvae.

in Table I.

Table I

Comparison of Mortality Counts of Larvae Placed at Room
Temperature and Those Placed in Refrigerator
for Four Weeks after Exposure

Temperature	Percent of Mortality of Larvae Placed at Room Temperature after Exposure	Percent of Mortality of Larvae Stored in Refrigerator 4 weeks after Exposure
-17½	10	6
-20	24	20
-22½	46	18
-25	58	24
-27½	48	38
-30	70	28
-32½	68	34
-35	66	48
Check	4.7	5

There was a lower mortality count among the larvae stored in the refrigerator for 4 weeks, after exposure, than among the larvae placed at room temperature immediately after exposure. This procedure did not obtain the desired results, as the same difficulty existed in separating the living larvae from the dead ones.

Although many of the larvae froze solid when exposed to the lowest temperatures, many showed signs of life when warmed up. A

test was made on February 18 and 19, 1937 to determine whether these frozen larvae would be able to continue development. Duplicate samples, of 50 each, of ponderosa pine larvae were exposed in petri dishes at 5° intervals. Half of the larvae were placed at room temperature, after exposure for mortality counts, as had been done in the previous experiments. The others were placed in 9 x 36 mm. vials (Figure 6) with fresh pine phloem, within several hours after the exposure period. The vials were closed with cotton and placed in 8-ounce ointment tins. The larvae that were not frozen soon started feeding on the phloem and developed into adults while the frozen ones were unable to feed even though they were alive. Those that were alive and unable to feed, gradually wasted away, some living as long as a month. Apparently the low temperatures injured some of the larvae beyond recovery. The results of this experiment are presented in Table II.

Table II

Comparison of Mortality Counts Obtained by
Noting Activity and Those Obtained by
Determining the Ability to Feed and Develop

Temperature	Percent Mortality of Larvae in Petri Dishes	Percent Mortality of Larvae in Vials with Phloem
-15	4	3
-20	4	18
-25	16	66
-30	40	100
-35	30	96
Check	5	0



Figure 6. Vials, size 9 x 36 mm., with phloem and pupae. The pupae developed from larvae placed in the vials two weeks earlier.

The mortality percents of the larvae in the vials are much higher than in the petri dishes because the permanently disabled larvae, which were living at the time the mortality counts of the larvae in the dishes were made, were not able to develop. For example, 60 percent of the larvae exposed at -30° showed life after being warmed to room temperature but actually none of the larvae were able to feed and develop. Apparently certain organs of the larvae are injured by the freezing and the larvae are not able to feed and continue development. Carter (1935) found that adults of Bruchus obtectus Say were unable to emerge after exposure to temperatures just below the limits of resistance, due to the loss of the insect's capacity to cut its way out of the bean.

The results of this preliminary test were so encouraging that the next two succeeding tests were also made with the vials and phloem to check with the old method of making activity counts in the petri dishes. The test on March 17 and 18, 1938, gave essentially the same results as the tests described above. The insects became active with the advance of the season and the April 27-30, 1938 tests showed similar mortality percents with both methods. This indicates that the feeding tests are necessary only during the winter, when the insects are dormant and more cold resistant. The feeding of a large number of larvae in individual vials entails a great deal of work but this method was used to determine mortality during the winters of the following two years, 1937 and 1938.

Relation of Cold-Hardiness to Season

During October and November the cold hardiness of the larvae increases very rapidly, reaching a maximum hardiness the first of December or very soon thereafter. They retain this maximum hardiness through December, January, and February. During March they start losing this cold-resistance, reaching their minimum cold-hardiness the last of April, at which time their hardiness is about equal to their hardiness at mid-October.

The critical ranges of the larvae from three hosts, ponderosa, limber, and lodgepole pine, are shown graphically in Figures 7-15. These figures show the critical ranges of the larvae through the fall, winter, and spring, starting with the first tests on October 13 (Figure 7) and ending with the last test on June 24 (Figure 15). The mortality curves are typically S-shaped. Mortality percent increases gradually during the first part of the critical range, more rapidly during the mid part of the range, and again gradually during the last part of the range. During midwinter the difference between the least and most hardy individuals in a sample may be as great as 25 degrees, but during the fall and spring before and after the larvae have reached their maximum degree of cold-hardiness the difference is not as great.

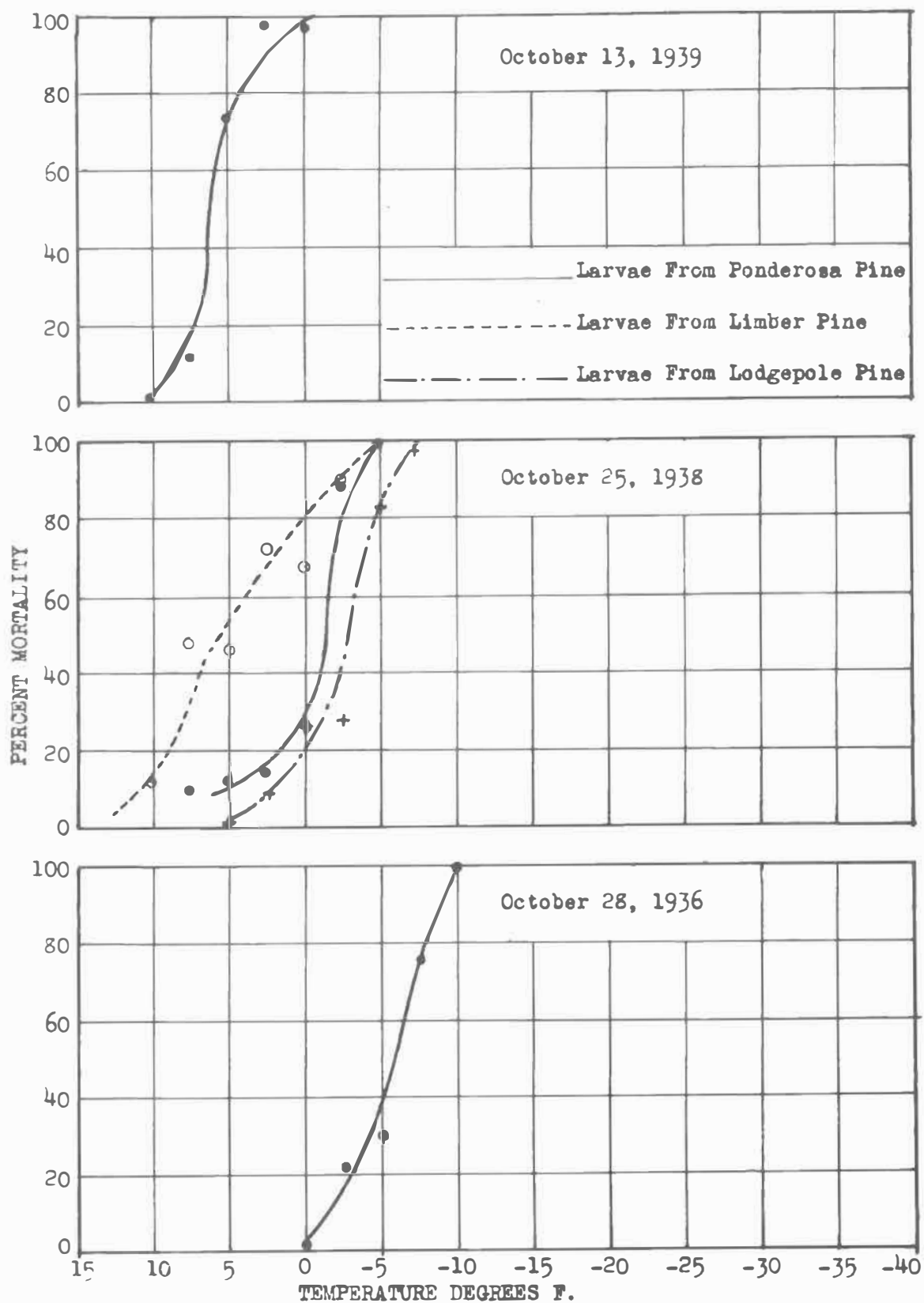


Figure 7. Relation of cold hardiness of larvae to season and host.

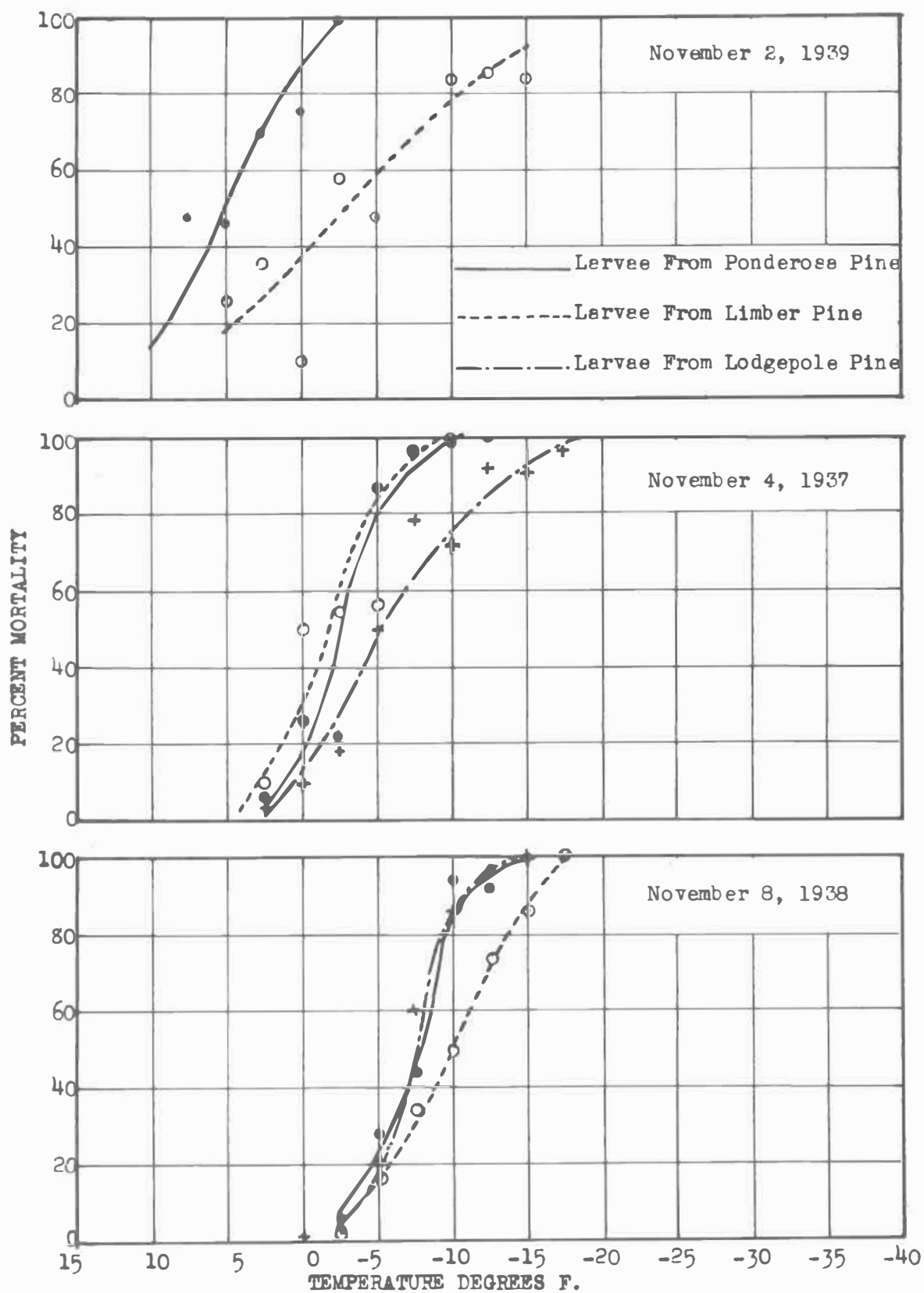


Figure 8. Relation of cold hardiness of larvae to season and host.

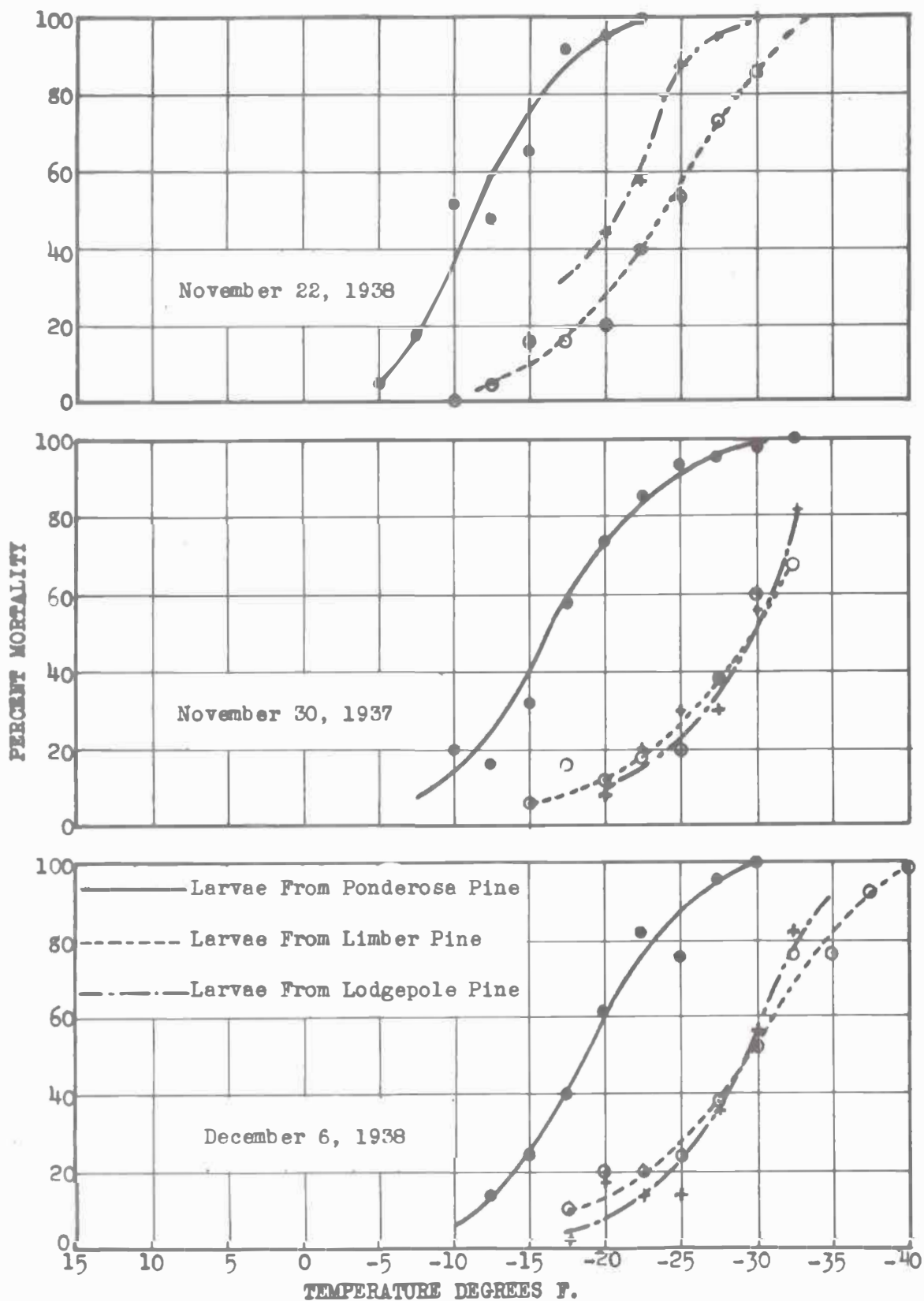


Figure 9. Relation of cold hardiness of larvae to season and host.

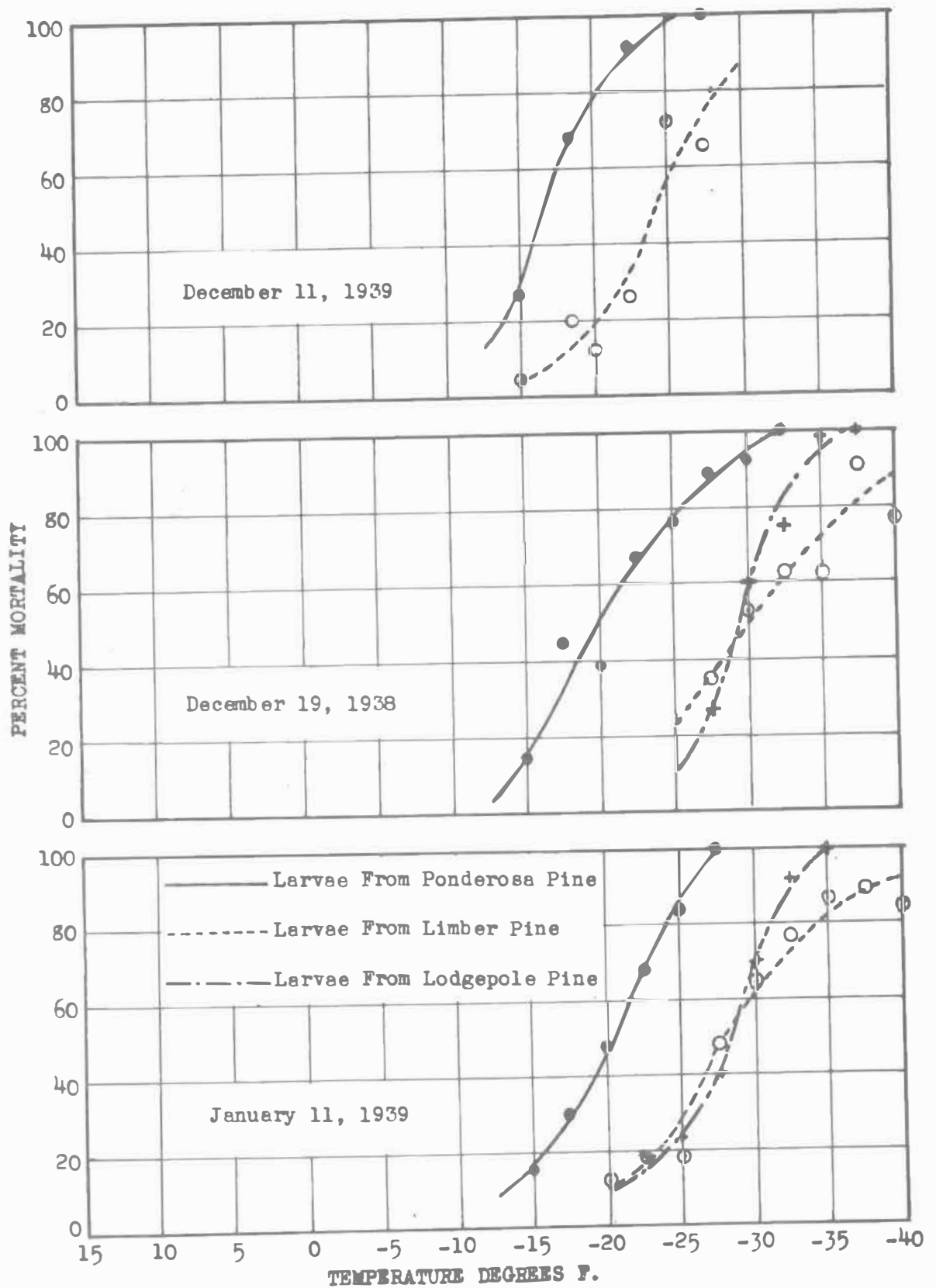


Figure 10. Relation of cold hardiness of larvae to season and host.

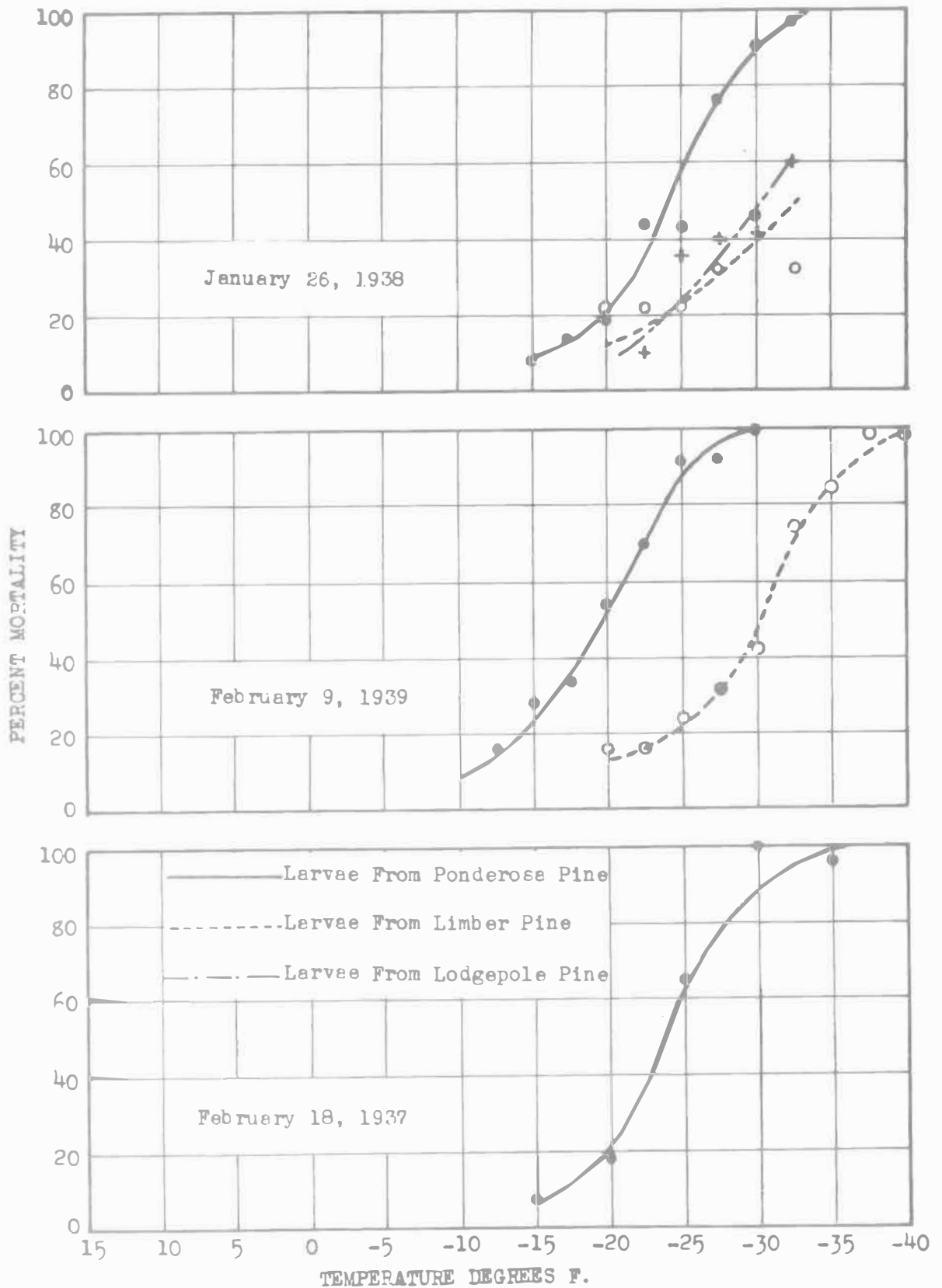


Figure 11. Relation of cold hardiness of larvae to season and host.

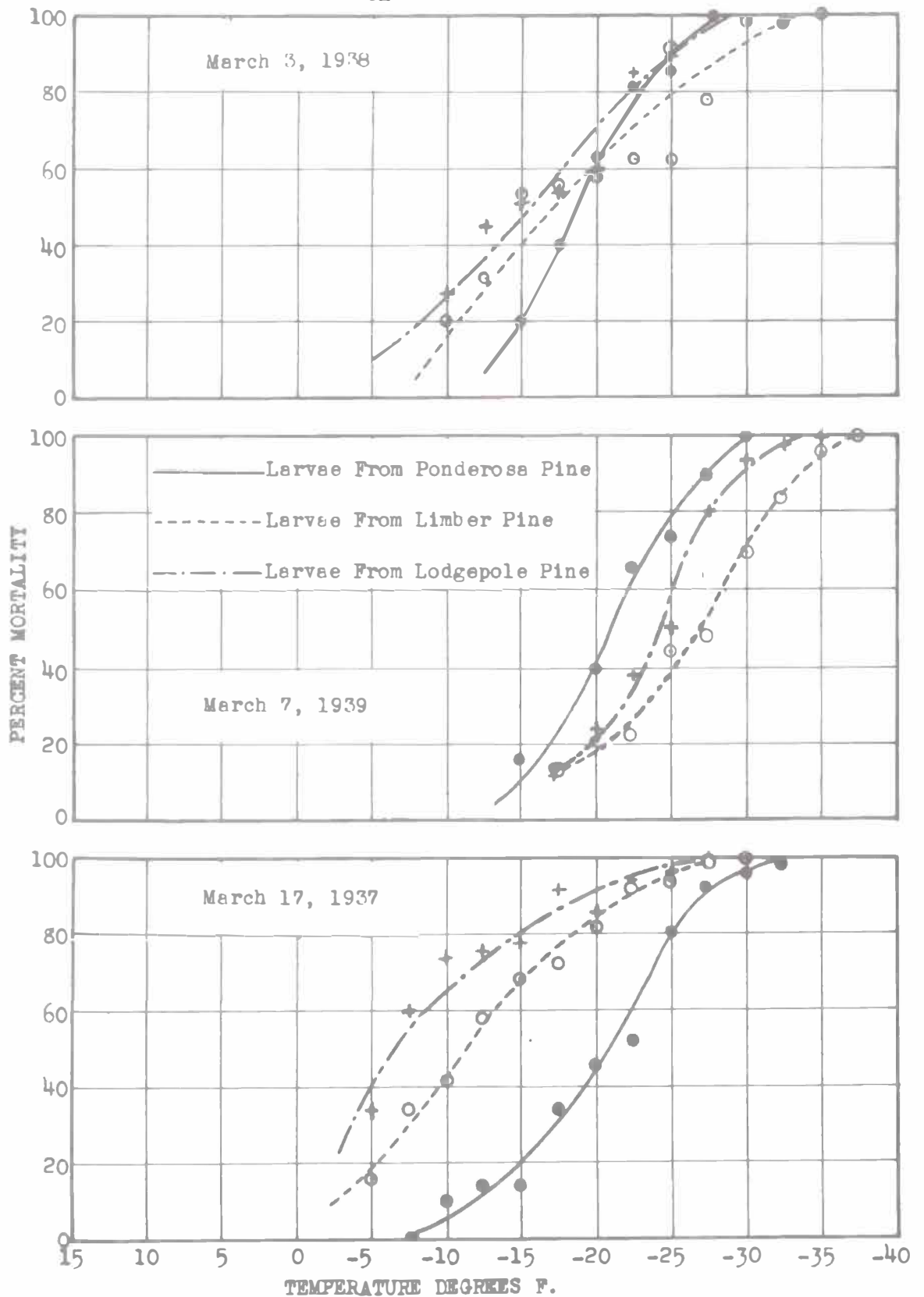


Figure 12. Relation of cold hardiness of larvae to season and host.

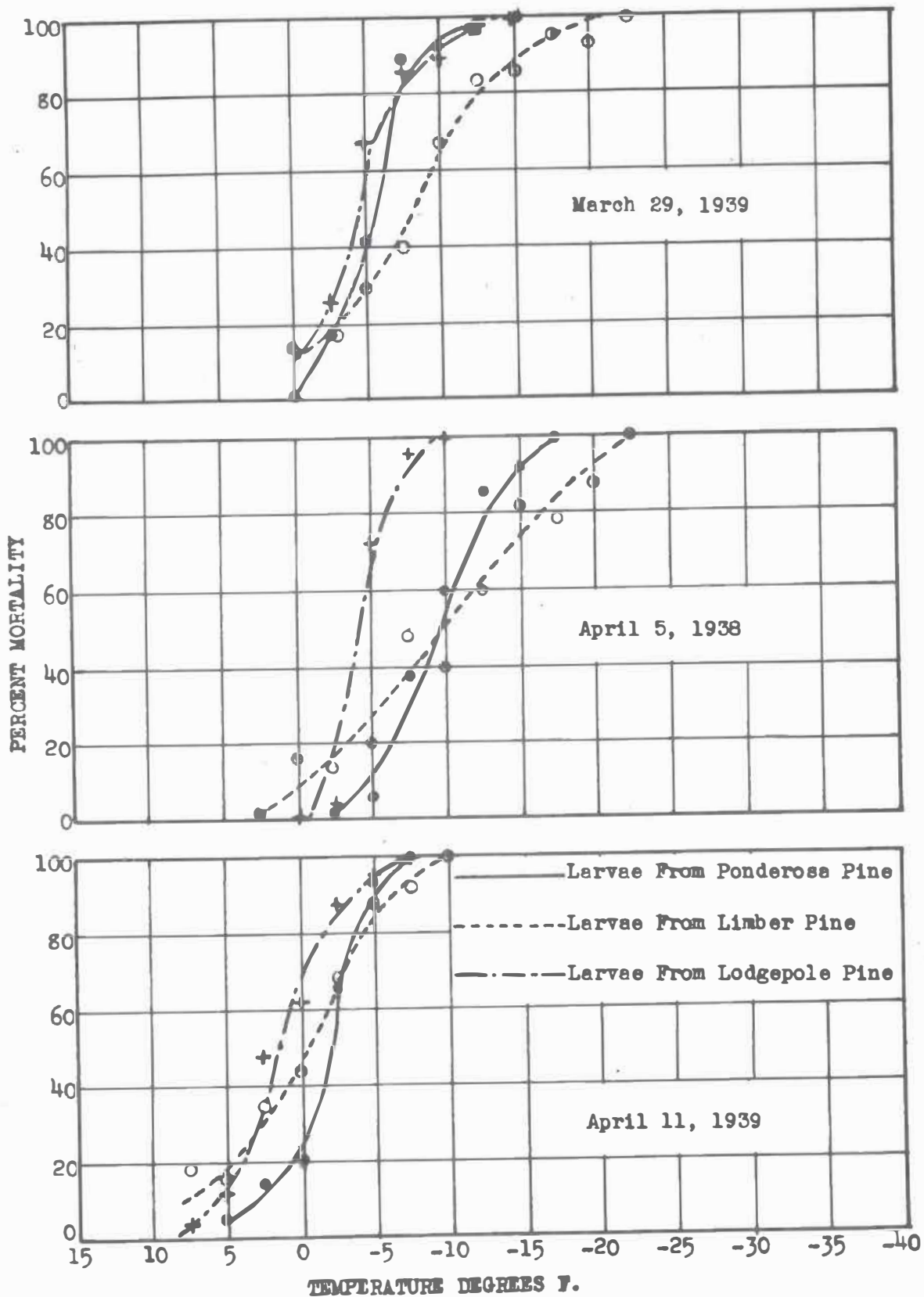


Figure 13. Relation of cold hardiness of larvae to season and host.

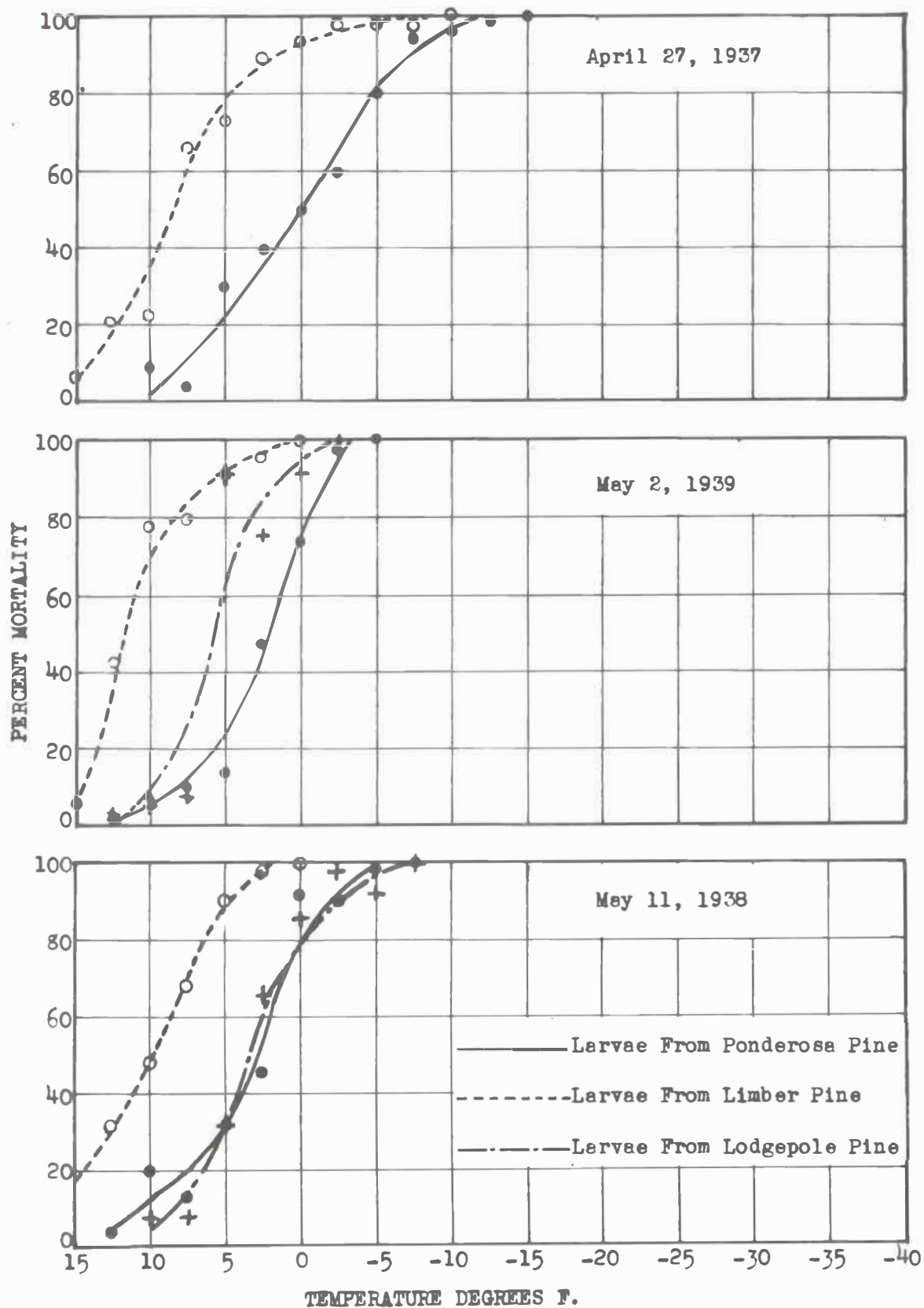


Figure 14. Relation of cold hardiness of larvae to season and host.

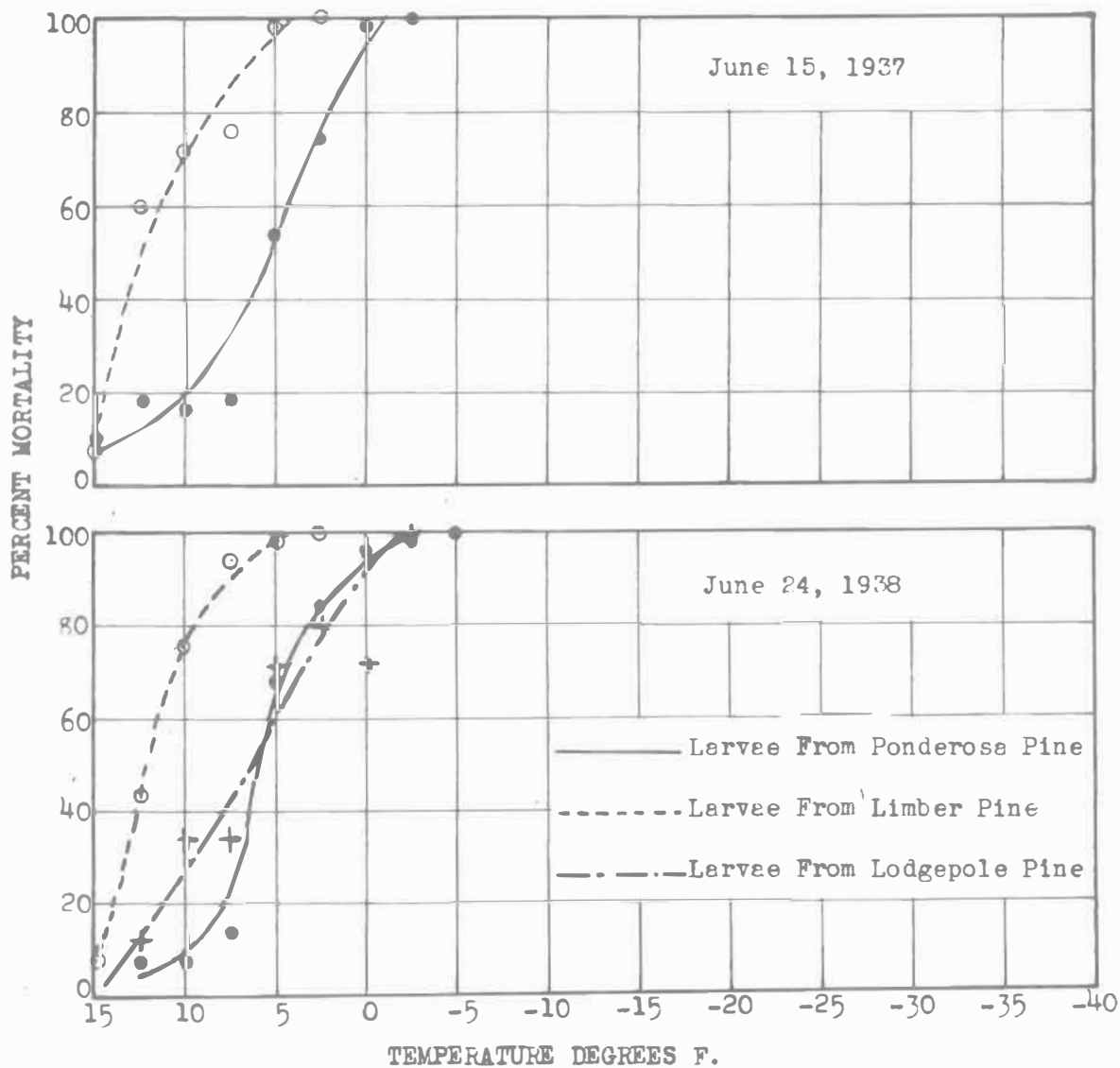


Figure 15. Relation of cold hardiness of larvae to season and host.

The results from all the experiments to determine the relation of cold-hardiness to season and hosts are summarized in graphical form (Figures 16 to 19). The data to make these charts were derived from the charts in Figures 7 to 15 inclusive. The lines representing initial, 50 percent, and 100 percent mortality are averages.

On October 13, the critical range of the ponderosa pine larvae was from 10° to -1° (Figure 16) and by mid-December, when the larva reaches its maximum cold-hardiness, the range was -13° to -31° . They retain this hardiness until soon after mid-March when they start losing this maximum hardiness. By the first of May their hardiness has decreased and ranges from 11° to -6° . During May and June their hardiness decreases very little as indicated by the fact that on June 24 the critical range was from 13.5° to -11° .

Figure 17 summarizes the critical range of larvae from limber pine. On October 23, when the first fall test was made, the critical range was from 12° to -5° but soon after the first of December their critical range had changed to -17° to -43° . The critical range remains constant through December, January, and February. Through March and April their hardiness decreases, reaching a minimum degree

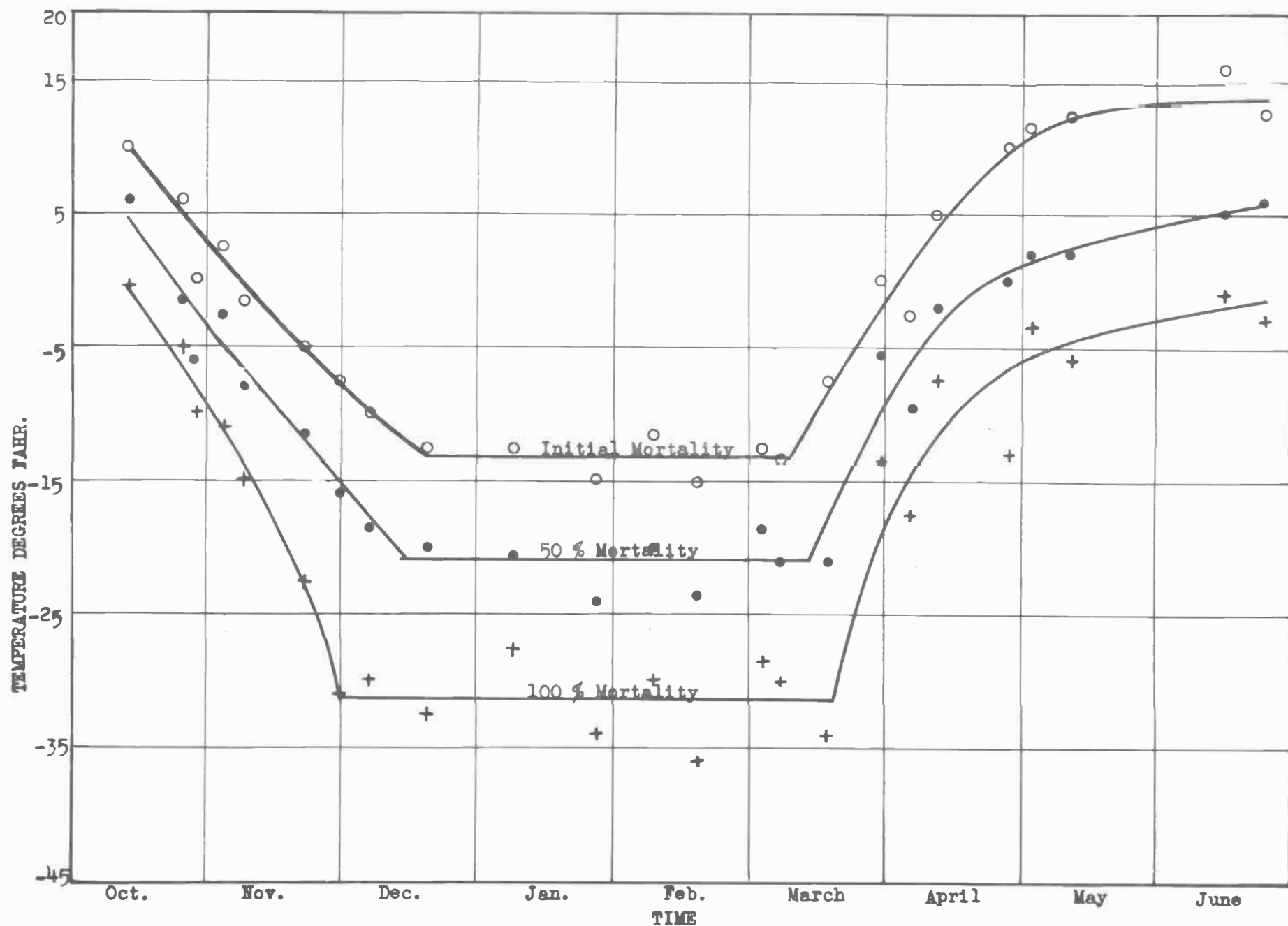


Figure 16. Critical low temperature range of larvae from ponderosa pine

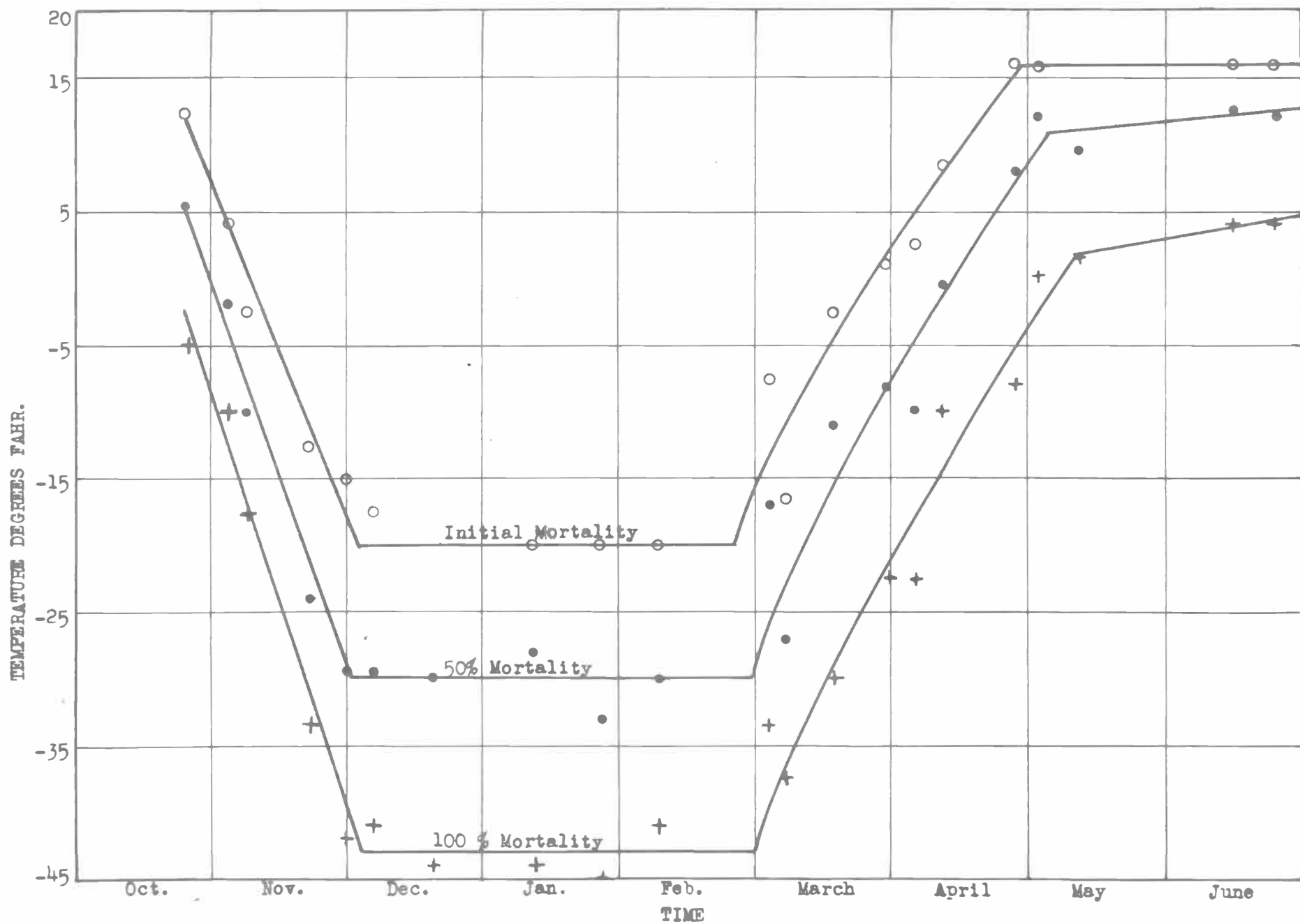


Figure 17. Critical low temperature range of larvae from limber pine

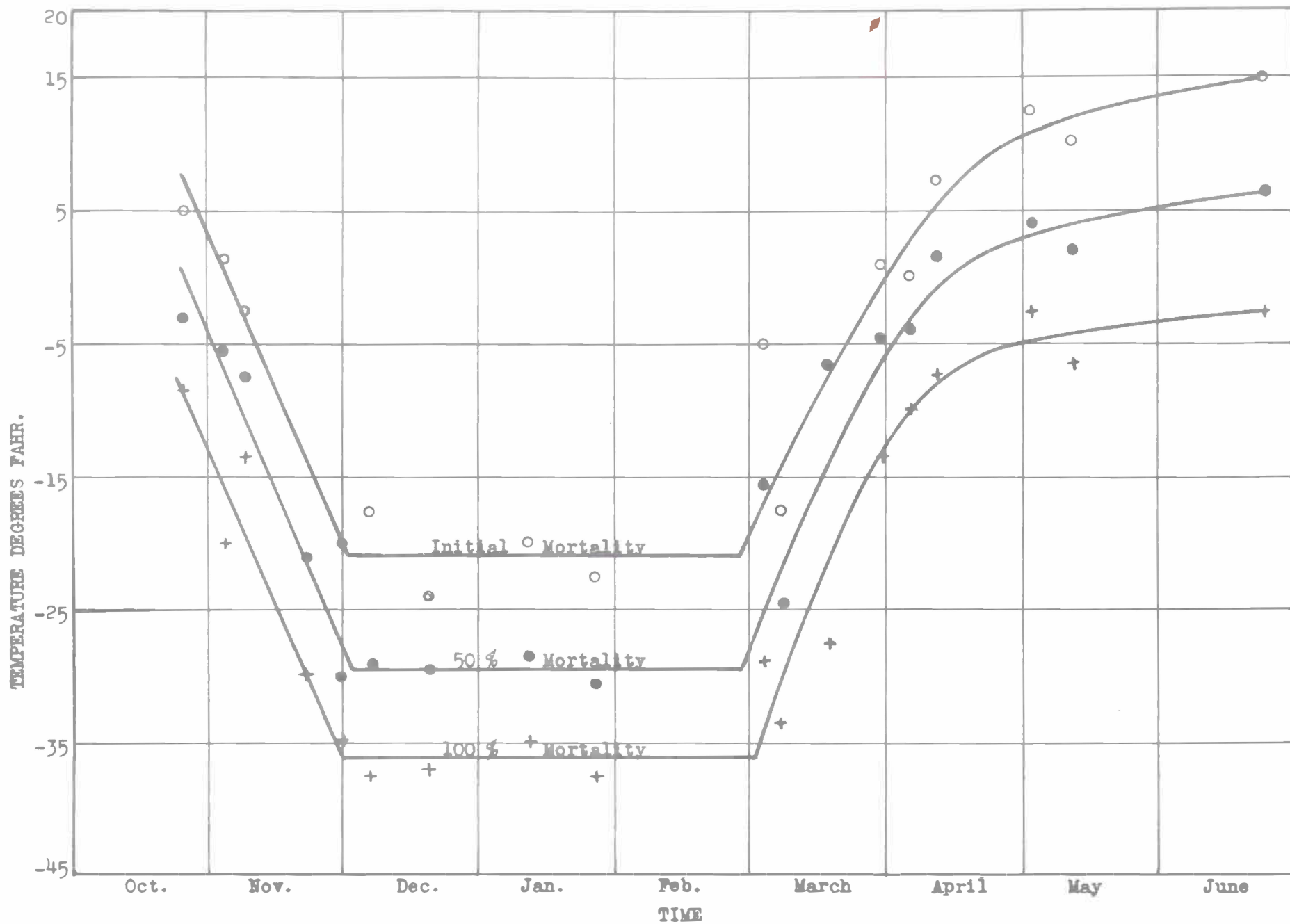


Figure 18. Critical low temperature range of larvae from lodgepole pine.

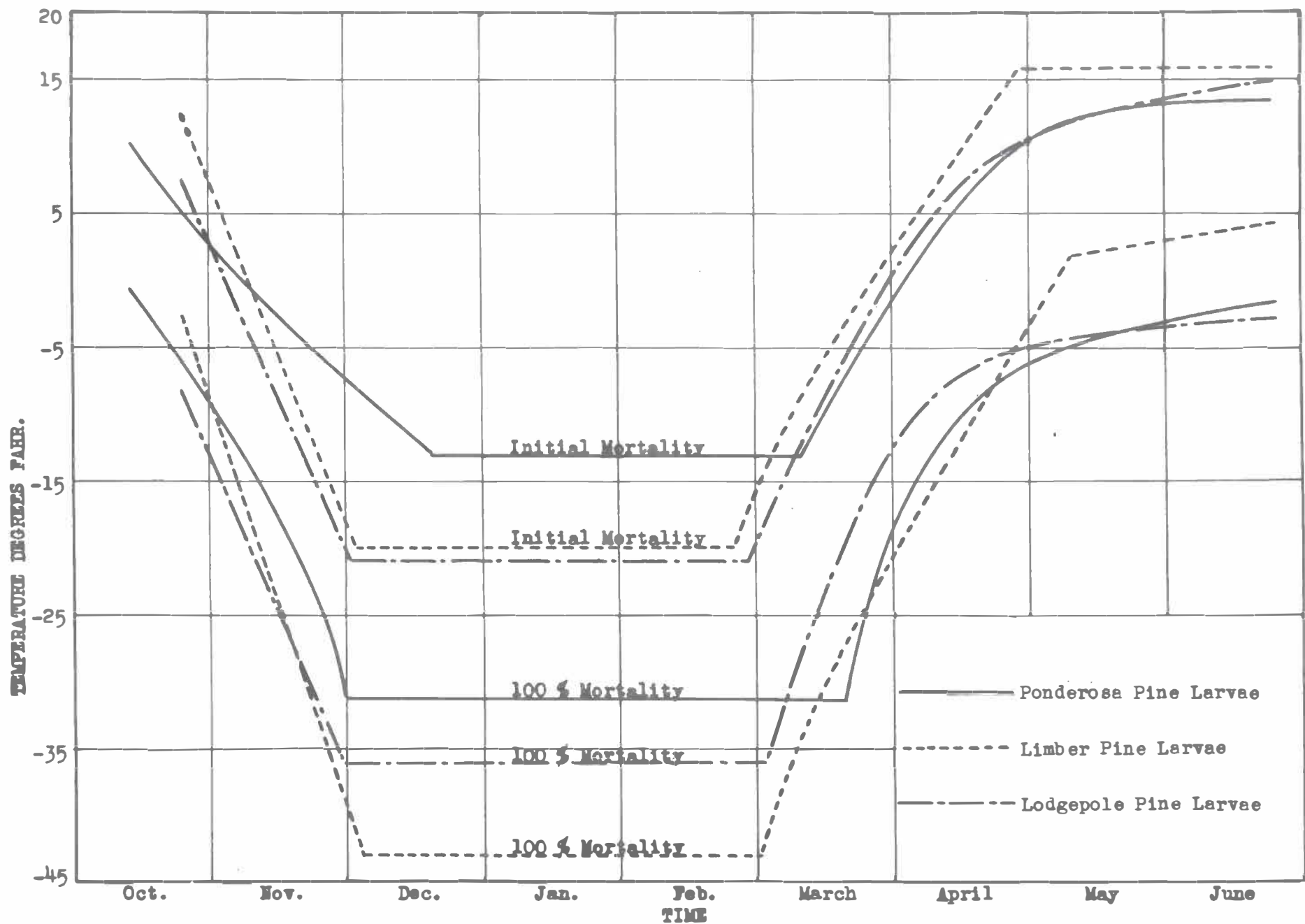


Figure 19. Comparison of critical low temperature range of larvae from ponderosa, limber, and lodgepole pine.

of hardness in May, at which time the critical range is 16° to 21° .

Figure 13 summarizes the critical range of larvae from lodgepole pine. On October 23 when the first fall test was made the critical range was 5° to -7° , but by the first of December the critical range was -21° to -36° . The critical range remained the same through December, January, and February. Through March and April their hardness decreases, and by the first of May the critical range was 10° to -5° . During May and June their hardness decreases very little.

It must be remembered that these curves were developed from the critical ranges of larvae stored at an elevation of approximately 8300 feet. At higher elevations the growing season is shorter and consequently the larvae probably harden earlier in the fall and lose the hardness later in the spring, although no tests were made to determine this.

The average maximum and minimum temperatures, obtained by a thermograph in the shelter for the infested logs, are compared with the seasonal hardness of ponderosa pine larvae in Figure 20. The temperature records are from November 1936 to May 1939 and give a general picture of the temperatures responsible for the changes in cold-resistance of the larvae. During the fall of the year,

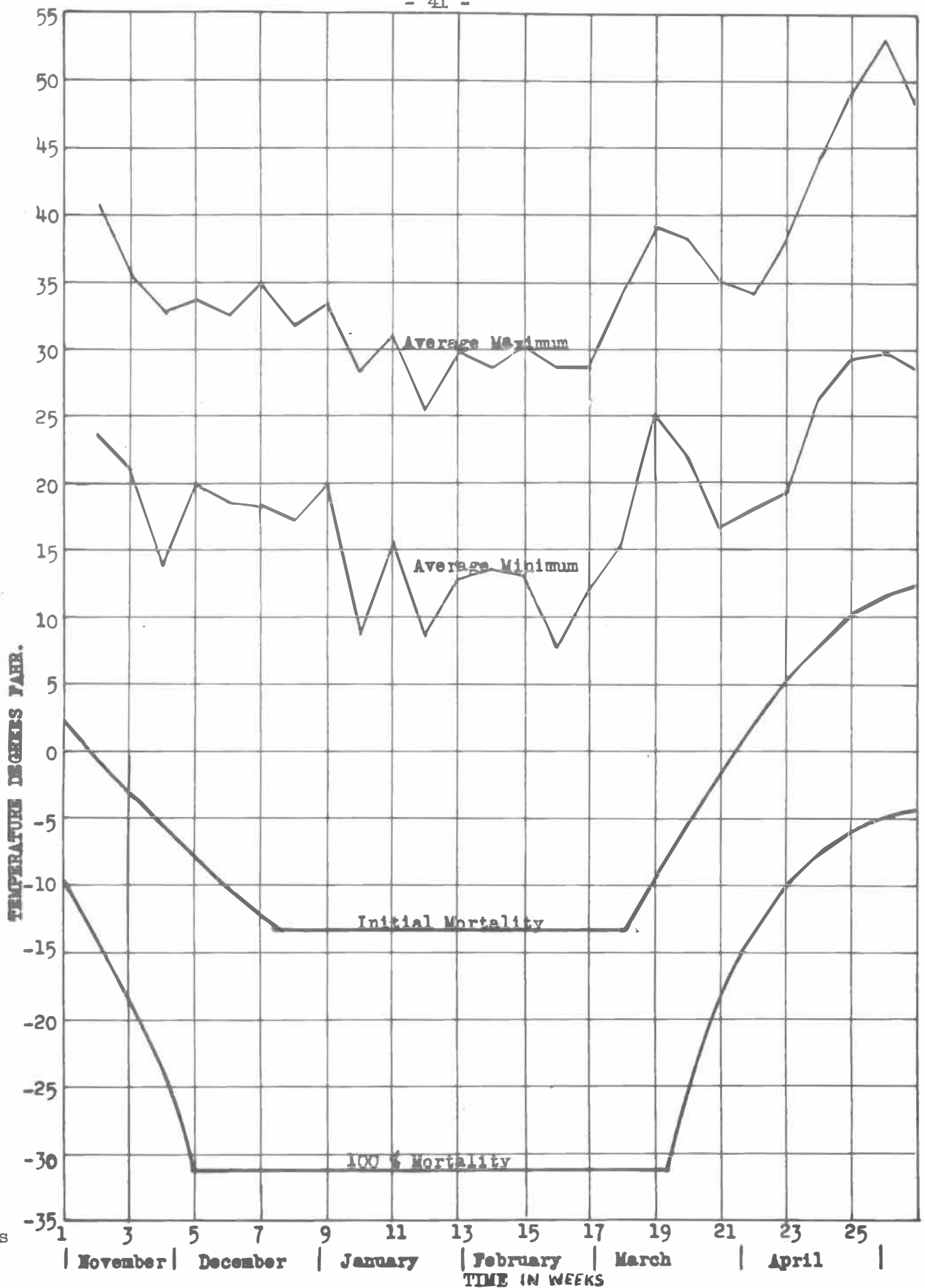
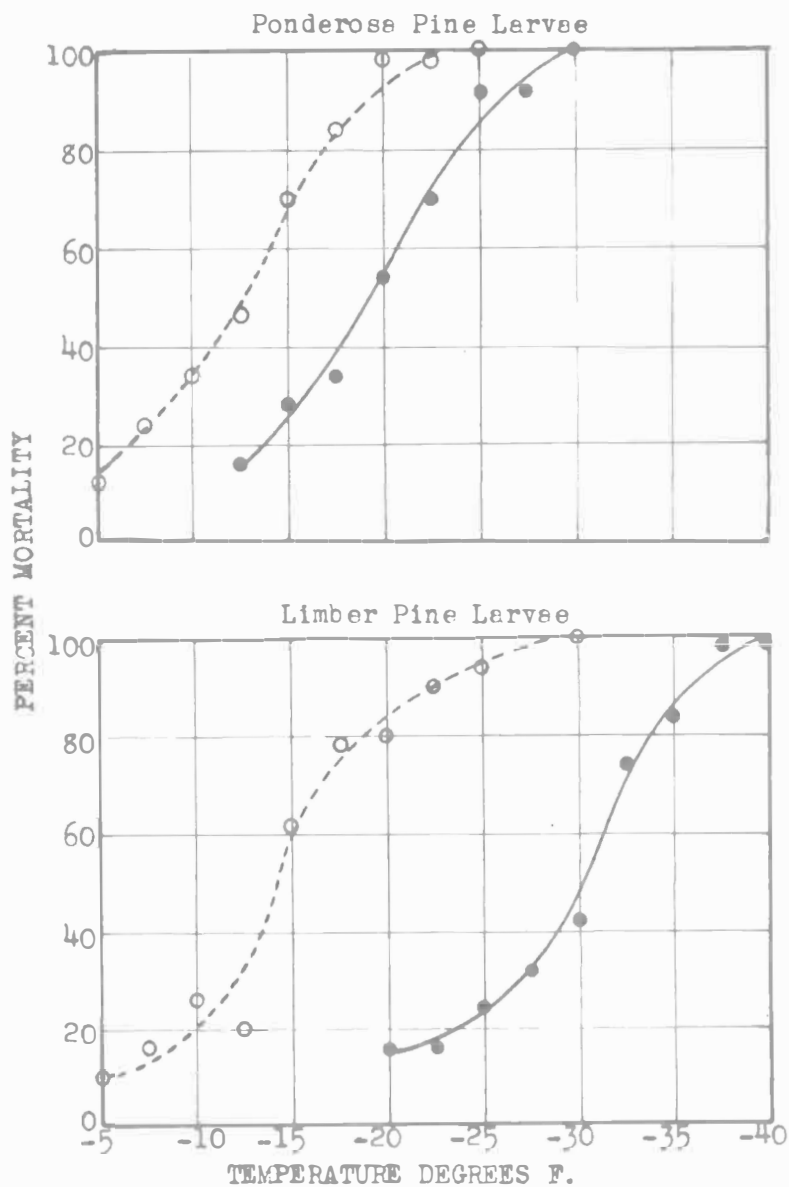


Figure 20. Comparison of average daily maximum and minimum temperatures to seasonal variation in critical range of the larvae from ponderosa pine.

with dropping temperatures, the larvae become more cold-resistant and during January and February, with a leveling off of the average maximum and minimum temperatures, the critical range of the larvae also levels off. With a general rise in temperatures during late February and March the critical range also rises. The critical range of the larvae from lodgepole and limber pine during March responds more quickly to temperature changes than the ponderosa pine larvae. This may be due, in part, to the thinner bark on the limber and lodgepole pine which allows subcortical temperatures to rise higher during the warm part of the day.

To determine the temperatures necessary to reduce the cold-resistance, several infested ponderosa and limber pine logs were placed in the refrigerator on January 21, 1939 and held at 36° until February 8, or a period of 18 days, when the larvae were removed from the bark and tested for cold-hardiness. Tests were also made, at the same time, of larvae taken from logs stored at natural outdoor temperatures. Figure 21 compares the critical range of these two groups. This conditioning reduced the hardiness of the ponderosa pine larvae an average of about 7° and the limber pine larvae about 15°. Another lot of infested logs was placed in the refrigerator on February 17, 1939 and held at 34° until March 6, 1939, also a period of 18 days, when the larvae were

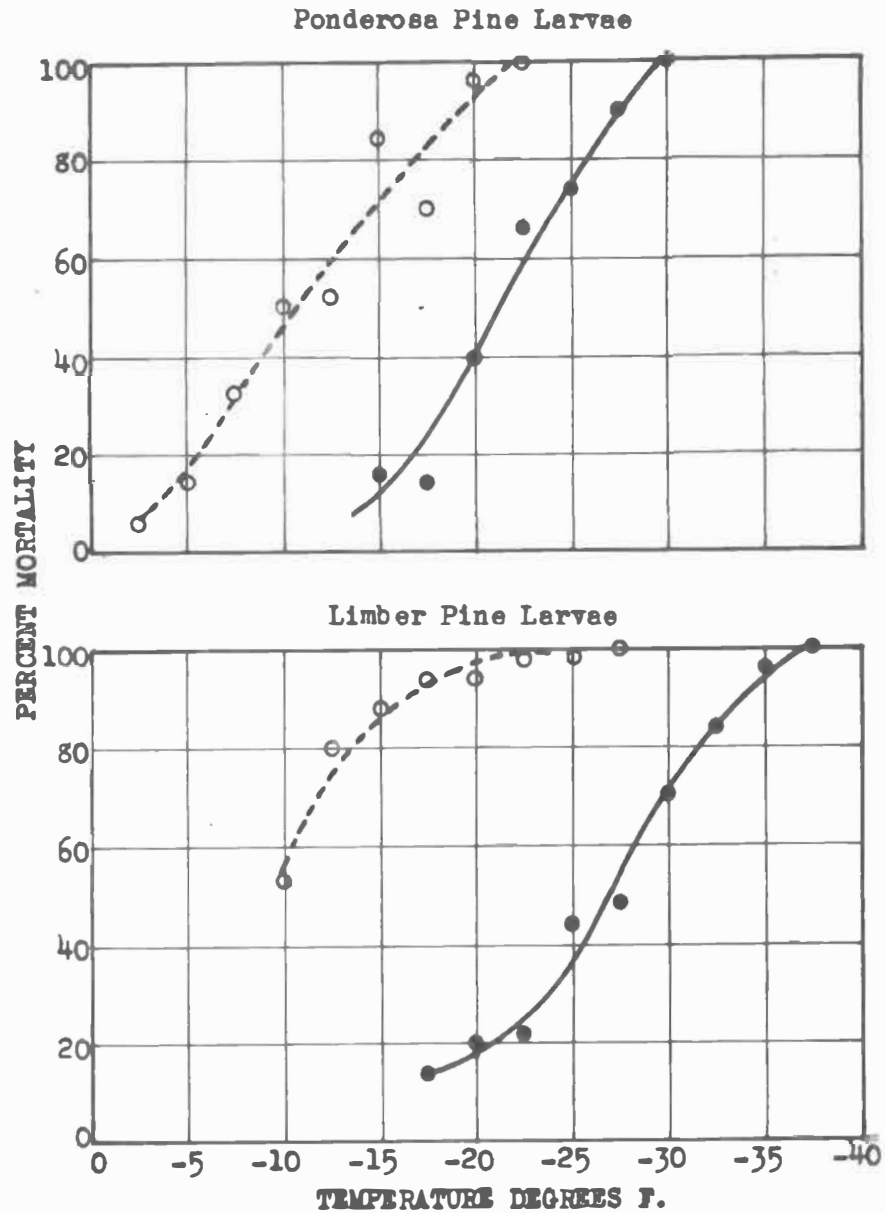
removed and tested for cold-resistance. The results of this test are presented in Figure 22. This conditioning reduced the cold-hardiness of the ponderosa pine larvae about 10° and that of the limber pine larvae approximately 17° below the cold-hardiness of the larvae stored at outdoor temperatures. The change in hardiness of the larvae stored at 34° was greater than in those stored at 36° but this may be due to the fact that the 34° test was made later in the winter season when changes had been initiated before the logs were placed at 34° . The experiments show that metabolism takes place at temperatures of 36° and 34° . It also illustrates the possibility of an unseasonable warm period in February or March reducing the cold-resistance, making the larvae more vulnerable to subsequent cold periods. It also shows that cold-resistance decreases before the larvae become active and take food.



--- Larvae stored at 36° from January 21, 1939 to February 8, 1939.

— Larvae stored at natural temperatures

Figure 21. Effects of storing the larvae at 36° for 18 days upon cold hardiness.



--- Larvae stored at 34° from February 17, 1939 to March 6, 1939

— Larvae stored at natural temperatures

Figure 22. Effects of storing the larvae at 34° for 18 days upon cold hardiness.

Since the first part of March marks the beginning of the decrease in hardness, the temperatures preceding and following this time are worthy of mention. The maximum daily temperatures during the three years varied, for the most part, between 28° and 44° during February and between 30° and 45° during March. Most of the daily minimum temperatures during the same time were between 0° and 25° during February and between 10° and 30° during March.

Relation of Cold-Hardiness to Host

During October and the first half of November the cold-hardiness of the larvae from the three hosts is similar, but during late November and early December the larvae from limber pine are the most hardy followed by lodgepole and ponderosa pine larvae. The order of hardness remains the same until May when the limber pine larvae become less hardy than those from the other two hosts. Figures 7-15 show the critical ranges of the three larval groups throughout the season. Figure 19 which was derived from Figures 16-18 inclusive, compares the critical ranges from the three hosts.

The variation of hardness of the ponderosa, limber, and lodgepole pine larvae is greatest during the winter (Figure 19). Although the initial critical range of lodgepole pine larvae during maximum hardness is about 1° lower than the limber pine

larvae, the 100 percent curve of the latter falls approximately 7° below the former.

Relation of Cold-Hardiness to Locality

During January and February 1938 cold-resistance tests were made on ponderosa pine larvae from four distant localities to determine whether or not there might be a difference in cold-hardiness due to locality or biological strains. The infested logs were collected in the field in 40-inch lengths, brought to Fort Collins by truck, and the larvae removed and tested as soon as possible after arrival.

The localities from which material was collected and the date tested were: Pine Lake in southern Utah, on the Powell National Forest near Panguitch, January 26-27; South Fork in southern Colorado on the Rio Grande National Forest, February 9-10; Black Hills near Ouster, South Dakota, on the Harney National Forest, February 9-10; and Redfeather Lakes in northern Colorado on the Roosevelt National Forest, January 26-27 and February 9-10 (Figure 1). The variation of environmental temperatures between these localities could not be determined. There were no applicable weather stations in the vicinities of the collection points.

The differences in hardiness at the four localities were not significant except that the Rio Grande National Forest larvae from southern Colorado were a little less hardy than the others.

Mortality percentages, obtained by exposing 100 larvae for 2 hours and 15 minutes at each $2\frac{1}{2}^{\circ}$ interval through the critical temperatures for the larvae, are given in Table III.

Table III

Comparison of Cold-Hardiness of Larvae from Ponderosa
Pine from Four Localities

Exposure Tempera- ture	Percent Mortality			
	Northern Colorado	Southern Colorado	Southern Utah	Black Hills of South Dakota
-15	12	18	9	
-17 $\frac{1}{2}$	14	32	17	24
-20	19	51	20	22
-22 $\frac{1}{2}$	29	61	34	38
-25	49	91	72	51
-27 $\frac{1}{2}$	90	98	81	65
-30	96	94	92	91
-32 $\frac{1}{2}$	100	100	100	98
Check	11	13	11	23

Surplus infested logs from the above localities were stored at Redfeather Lakes, and the larvae tested again for cold-hardiness on May 11, but again there was no significant difference in their cold-hardiness.

Tests with larvae from the Black Hills of South Dakota and northern Colorado were again made on November 28, 1938. At that time the northern Colorado larvae were approximately $2\frac{1}{2}^{\circ}$ more hardy than those from the Black Hills.

The fact that the hardiness of the larvae from the four localities was nearly the same during midwinter does not necessarily mean that their hardiness during the fall and spring would be the same. Hardiness during fall and spring, when their cold-resistance is changing, would probably vary in proportion to the coldness of the local weather.

Relation of Mortality to Period of Exposure

Several tests were made to determine whether mortality increased with longer exposures to cold. The first tests were made with ponderosa pine larvae during the period March 15-22, 1938. Six petri dishes, containing 50 larvae each, were placed in the low temperature cabinet at the same time and the cabinet held at a uniform temperature. One dish of larvae was taken out at the end of the following periods: 1, 2, 4, 6, 12, and 24 hours. The results of this test are presented in Table IV. There was a large difference in the mortality between larvae exposed 1 hour and 2 hours, but there appeared to be no significant difference in the mortality of those exposed for a period of 2 hours up to 24 hours except possibly with the exposures at -5° and -7° . In these cases 24-hour exposures appeared to produce additional mortality. The failure of the 1-hour exposures to produce mortality as great as the 2-hour exposures may be because the temperature inside the petri dish does not reach that of the cabinet within 1 hour.

Table IV

Relation of Mortality to Period of Exposure,
March 15-22, 1938

Exposure Tempera- ture	Exposure Period and Percent Mortality						
	Check	1 Hour	2 Hours	4 Hours	6 Hours	12 Hours	24 Hours
-5	12	10	16	16	26	22	28
-7½	—	8	4	14	8	14	30
-10	—	20	56	56	40	58	58
-12½	—	26	83	82	84	62	86
-15	6	42	86	100	92	84	92
-20	—	60	92	100	96	100	98
-25	6	83	100	100	100	100	100

Three additional tests, two in the spring when the larvae were active and one in the fall, were made to determine whether the conclusions drawn from the tests of March 15-22 (when the larvae are dormant) would apply to all seasons. The results of these tests are shown in Tables V, VI, and VII. In these tests samples of 100 larvae were used for each period of exposure.

Table V

Relation of Mortality to Period of Exposure,
April 18-20, 1939

Exposure Temperature	Exposure Period and Percent Mortality				
	2 Hours	4 Hours	8 Hours	12 Hours	24 Hours
0	23	17	22	30	35
-2½	40	59	65	61	65
-5	70	86	83	82	85

Table VI

Relation of Mortality to Period of Exposure,
May 4-9, 1939

Exposure Temperature	Exposure Period and Percent Mortality					
	Check	2 Hours	4 Hours	8 Hours	12 Hours	24 Hours
2½	4	17	24	35	27	36
0	—	44	85	69	62	63
-2½	3	88	96	95	96	91
-5	—	100	100	100	100	100

Table VII

Relation of Mortality to Period of Exposure,
November 6-7, 1939

Exposure Temperature	Exposure Period and Percent Mortality			
	2 Hours	4 Hours	12 Hours	24 Hours
-5	23	24	51	67
-10	71	73	68	90

The results in Tables V and VI indicate that there is some additional mortality produced by longer exposures, particularly at temperatures in the upper part of the critical range.

The results in Table VII indicate rather conclusively that during the fall of the year the longer exposures are more lethal. For example, at -5° , 2 hours exposure produced 23 percent mortality while 24 hours produced 57 percent mortality. Likewise at -10° , exposure for 2 hours produced 71 percent mortality while 24 hours produced 90 percent mortality.

Since low temperatures in nature nearly always occur early in the morning and are apt to be for very short periods, this additional mortality produced by long exposures is not likely to occur in the field.

Effect of Rate of Temperature Change

Temperature changes in the field are gradual compared to the sudden changes the larvae are subjected to when they are placed in the cabinet at very low temperatures and later removed from the cabinet to room temperature. Several tests were made to determine whether these sudden changes have detrimental effects.

On April 21, 1939, 250 larvae were placed in the refrigerator at 50° and the temperature gradually lowered to -4° over a period of $5\frac{1}{2}$ hours, at which time 250 additional larvae were put into the cabinet. The cabinet was held at -4° and at the end of 10

hours the larvae were removed. There was a 20 percent mortality among the larvae that were gradually cooled and a 17 percent mortality among those suddenly cooled.

On January 26-27, 1938, duplicate samples of 50 larvae each were exposed at each 2 degree interval over the critical range. Upon being removed from the refrigerator one sample was placed at 32° for 2 hours and 15 minutes before being placed at room temperature and the other sample was left at room temperature. The results of this experiment are in Table VIII.

Table VII

Comparison of Gradual and Sudden Warming of
Dominant Larvae after Exposure to Low
Temperature, January 26-27, 1938

Exposure Temperature	Percent Mortality	
	Larvae Placed at 32° after Exposure	Larvae Placed at Room Temperature after Exposure
-20	22	16
-22½	32	56
-25	34	52
-27½	82	70
-30	91	90
-32½	100	94
Check	16	--

A similar test was made April 11-13, 1939. After removal from the cabinet the larvae were left at 32° for 24 hours instead of 2 hours and 15 minutes. The results of this test are presented in Table IX.

Table IX

Comparison of Gradual and Sudden Warming of Active Larvae after Exposure to Low Temperatures, April 11-13, 1939

Exposure Temperature	Percent Mortality	
	Larvae Placed at 32° after Exposure	Larvae Placed at Room Temperature after Exposure
7½	4	6
5	6	4
3½	14	14
0	22	20
-2½	70	62
Check	8	--

From the percent mortality obtained by the sudden and gradual temperature changes it is evident that sudden changes are not detrimental to the larvae. Similar conclusions were made by Miller (1951) who found that the time required to return to normal temperatures did not affect the mortality of the western pine beetle.

Relation of Cold-Resistance to Stage of Development

The Black Hills beetle normally overwinters in the larval stage and this is therefore the only stage subject to the effect of freezing temperatures. However, to make the experiment more complete, tests were made March 19-24, 1937 with larvae, pupae, and adults reared in the greenhouse; on June 15-17, 1937 on larvae and pupae collected in the field; and also on June 24-25 with field material.

The pupae are the hardiest followed by the larvae and adults (Table X). The pupal and adult critical range is characteristically shorter than the larval range. The pupae were 5° to $7\frac{1}{2}^{\circ}$ more cold-hardy than the larvae and the adults approximately $2\frac{1}{2}^{\circ}$ to 5° less hardy than the larvae. The insects reared in the greenhouse were also less hardy than those collected in the field.

Table X

Comparison of Critical Ranges of Larvae,
Pupae, and Adults

Date of Test:		Ponderosa Pine			Limber Pine		Lodgepole Pine		
		Larvae	Pupae	Adults	Larvae	Pupae	Larvae	Pupae	Adults
March 19-24, 1937	Initial ^{1/}	17½	10	17					
(Greenhouse reared)	Ultimate ^{2/}	2	-2	0					
June 15-17, 1937	Initial	15	5						
(Field collected)	Ultimate	-2	-5						
June 24-25, 1938	Initial	10	2	12	15	7	13	2	12
(Field collected)	Ultimate	-5	-5	5	2	-5	2	-5	2

1. Initial point is that temperature at which mortality is first perceptible, or the beginning of the critical range.
2. Ultimate point is that temperature at which mortality is complete, or the end of the critical range.

Relation of Contact Moisture to Mortality

Moisture in contact with insects affects their undercooling point and survival at low temperatures. This has been observed by a number of workers. Beal (1933) found that the larvae of the southern pine beetle, in the wet phloem, were killed at higher temperatures

than those in the outer dry bark. Miller (1931) found that there was a perceptible lowering of resistance of the western pine beetle in bark saturated with water. In studying the effects of subzero temperatures on the western pine beetle Keen and Furniss (1937) found that mortality was highest among the larvae in the phloem. Mortality decreased in the larvae in proportion to their distance from the phloem. The moisture on the body of the insect inoculates the body fluids causing them to freeze at higher temperatures (Hodson 1937 and Salt 1936).

There was a perceptible lowering of resistance of the Black Hills beetle larvae when in contact with wet blotting paper. Samples of 50 larvae from limber pine were placed in contact with wet blotting paper before exposure and another sample exposed in the usual way (Table XI). The contact moisture decreased the resistance of the larvae approximately 4 or 5 degrees.

Table XI

Effect of Contact Moisture upon Freezing and
Survival of Active Larvae, April 11-13, 1939

Exposure Temperature	Percent Mortality	
	Larvae Dry	Larvae in Contact with Wet Blotter
7	18	50
5	16	60
2½	34	60
0	44	74
-2½	66	76
-5	88	86

A test with larvae from limber pine was again made on May 2-5, 1939 in which 100 larvae were used in each sample. The results of this test showed that the wet larvae were approximately 3 degrees less resistant than the dry larvae (Table XII) in the higher temperatures of the critical range, but in the lower temperatures there was very little if any difference in resistance.

Table XII

Effects of Contact Moisture upon Freezing and Survival of Active Larvae, May 2-3, 1939

Exposure Temperature	Percent Mortality	
	Larvae Dry	Larvae in Contact with Wet Blotter
20	1	3
17½	2	17
15	6	24
12½	43	60
10	78	86
7½	80	89
5	92	96
2½	96	97
0	100	100

On April 24, 500 larvae from ponderosa pine were exposed at -4° , half of which were placed on wet blotting paper and half handled in the usual way. Mortality of 93.6 and 82.8 percent respectively occurred. These experiments were made with active larvae which are least cold resistant. With cold-hardened larvae the effects of contact moisture may be different.

Since the phloem, in which the larvae of the Black Hills beetle exist, varies in moisture content with individual trees and hosts, the effects of lethal low temperatures under natural conditions would also vary. The phloem of infested limber pine is frequently wet while the phloem of ponderosa and lodgepole pine is usually quite dry. The phloem in trees with advanced brood is apt to be drier than that in trees with less advanced brood.

Relation of Sex to Cold Resistance

The male and female of the Black Hills beetle appear to be equal in cold-hardiness. Sex counts were made on the adults that developed from larvae that survived exposures to low temperatures. The total number of beetles and the percent females are given in Table XIII. In order to get a larger sample the adults were used from 4 tests made during extreme hardiness during December 1938 and January, February, and March 1939.

There was a higher percent survival of females at the lower temperatures of the critical range but this probably can be attributed to inadequate samples at those exposures. It is interesting to note

the sex-ratio of this particular insect and its variation by host. The adults from limber pine were 53 percent female, those from ponderosa 58 percent, and those from lodgepole pine 60 percent.

Table XIII

Relation of Sex to Cold-Resistance

Exposure Temperature	Ponderosa Pine		Limber Pine		Lodgepole Pine	
	Total No.		Total No.		Total No.	
	Adults Survived	Percent Female	Adults Survived	Percent Female	Adults Survived	Percent Female
-12½	57	61				
-15	127	55				
-17½	126	56	66	39	54	56
-20	90	57	135	59	56	54
-22½	54	59	121	55	81	63
-25	34	56	119	51	74	62
-27½	12	83	82	54	57	53
-30			66	40	27	52
-32½			34	59	12	92
-35			22	68		
-37½			9	56		
-40			8	87		
Check	119	63	150	54	64	61
Total	619	Av. 58	314	Av. 53	415	Av. 60

Relation of Air and Subcortical Temperatures

Subcortical temperatures in ponderosa pine lag behind air temperatures and the lag varies directly with the bark thickness (Beal 1934). Upon the prediction of subzero weather in the field Beal placed mercurial thermometers under the bark of ponderosa pine infested with the western pine beetle in Oregon and made hourly readings through the cold period. From 4 A.M. of the first day to 7 A.M. of the following day, the air temperature dropped from 25° to -26°, or approximately at the rate of 2° per hour. The minimum temperatures under the bark were: -17° and -18° under bark 1/2 inch thick; -5° to -8° under bark 1 inch thick; -4° under bark 1 1/8 inches thick; and 1° under bark 1 1/2 inches thick. Thus the importance of bark thickness in regulating subcortical temperatures can readily be seen.

The Black Hills beetle is found beneath the bark of limber, lodgepole, and ponderosa pine, and the insulating values of this bark must be known to determine the air temperatures necessary to produce lethal temperatures beneath the bark.

The subcortical temperature measurements were made with thermocouples placed beneath the bark. Small log sections approximately 12 inches long were cut from infested trees and the ends of the logs coated with hot paraffin wax. The couples were placed beneath

the bark and the sections placed in the low temperature cabinet. The thermocouple junction was inserted from the end of the cross-section through the phloem to a depth of approximately 4 inches. This deep insertion prevented an error in reading which might otherwise occur with a shallow insertion due to conduction of heat through the wires from the warmer subcortical temperatures to the colder air temperatures. After the log sections were placed in the cabinet and after the temperature became stabilized at 30° , the air temperature was lowered at a uniform rate and temperature measured at hourly intervals.

There are a number of variables in field conditions that affect the relation between air and subcortical temperatures, making it impossible to duplicate outdoor conditions in the cabinet. Some of these are rate of drop and the lack of uniformity in the rate of drop. For example the temperature may drop 10 degrees in one hour and not at all the second hour and again during the third hour it may start dropping again. The subcortical temperature before the cold period started would also somewhat determine the minimum subcortical temperature. For example, if the air temperature reached a minimum of -30° , the minimum subcortical temperature would be influenced by the heat stored up in the tree. Rate of air movement would also affect the lag of subcortical temperatures.

For the most part the thickness of ponderosa pine bark under which the Black Hills beetle works varies from approximately 1/4 to 1 inch. The limber pine bark is thinner than ponderosa pine and most of it is 1/2 inch or less in thickness. Lodgepole pine bark is extremely thin and is usually approximately 1/4 inch in thickness.

The results of the test are shown graphically in Figures 23-30. In Figure 23 the temperature was lowered 40° from a temperature of 30° to -10° during a period of 12 hours. This represents a drop of $3 \frac{1}{3}^{\circ}$ per hour. The temperature beneath the ponderosa pine bark 7/8 inch thick lagged approximately $3 \frac{1}{2}$ hours behind the air temperature; the temperature beneath the 3/8 inch limber pine bark lagged approximately $2 \frac{3}{4}$ hours; the temperature beneath the 1/2 inch and 3/8 inch ponderosa pine bark lagged approximately 2 hours; and the lag was approximately 2 hours for the 3/16 inch lodgepole pine bark. The differences between air and subcortical temperatures during the drop were: ponderosa pine bark 7/8 inches thick 11° ; 3/8 inch thick limber pine bark 8.8° ; the 1/2 inch and 3/8 inch ponderosa pine bark 6.8° , and the 3/16 inch lodgepole pine approximately 6.8° . Figure 24 also represents a 40° drop in 12 hours but a different set of log sections of different bark thicknesses was used. The lag in time and differences in temperature were similar to those in Figure 23.

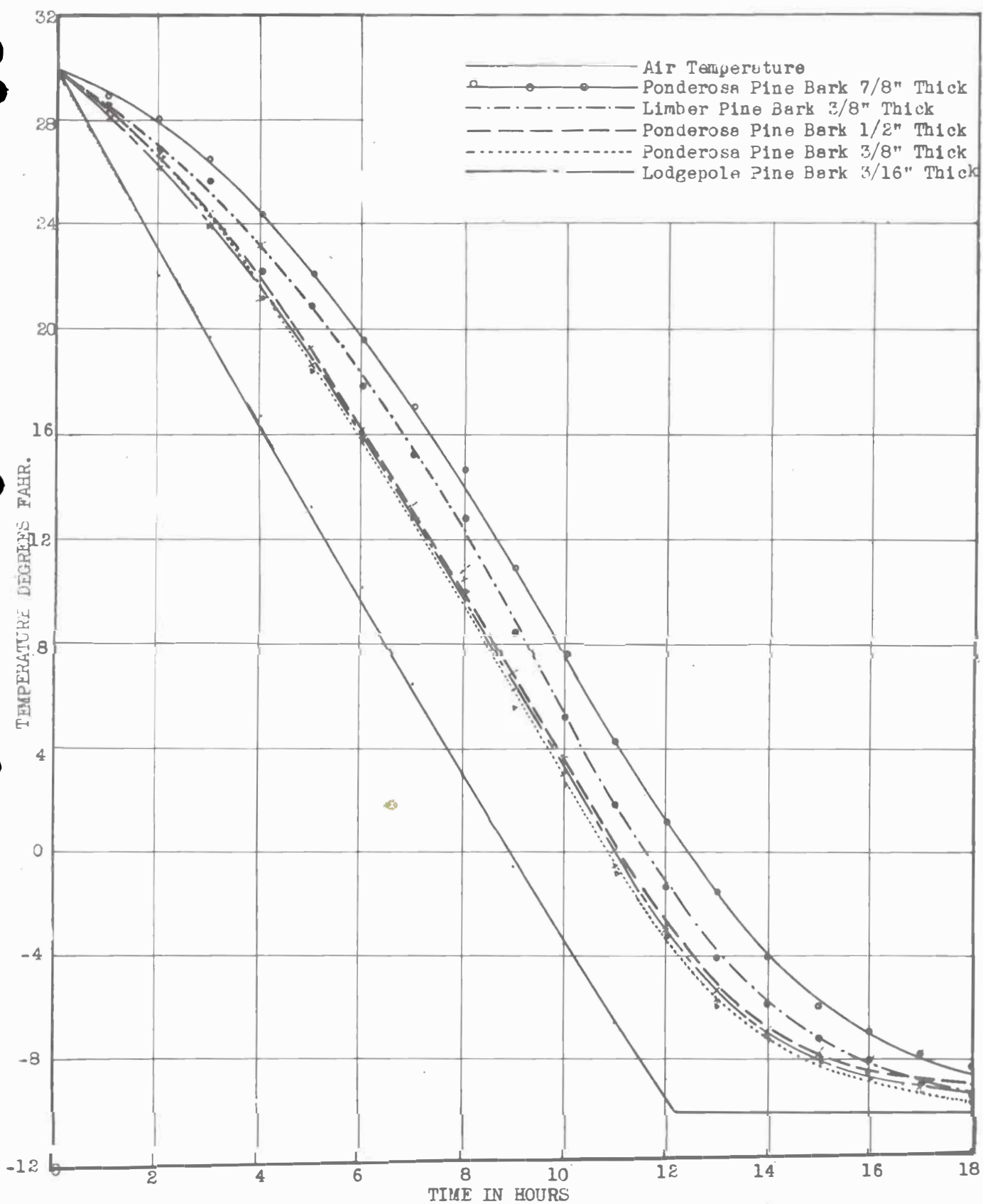


Figure 23. Relation of subcortical temperatures to air temperature during a 40° drop in 12 hours.

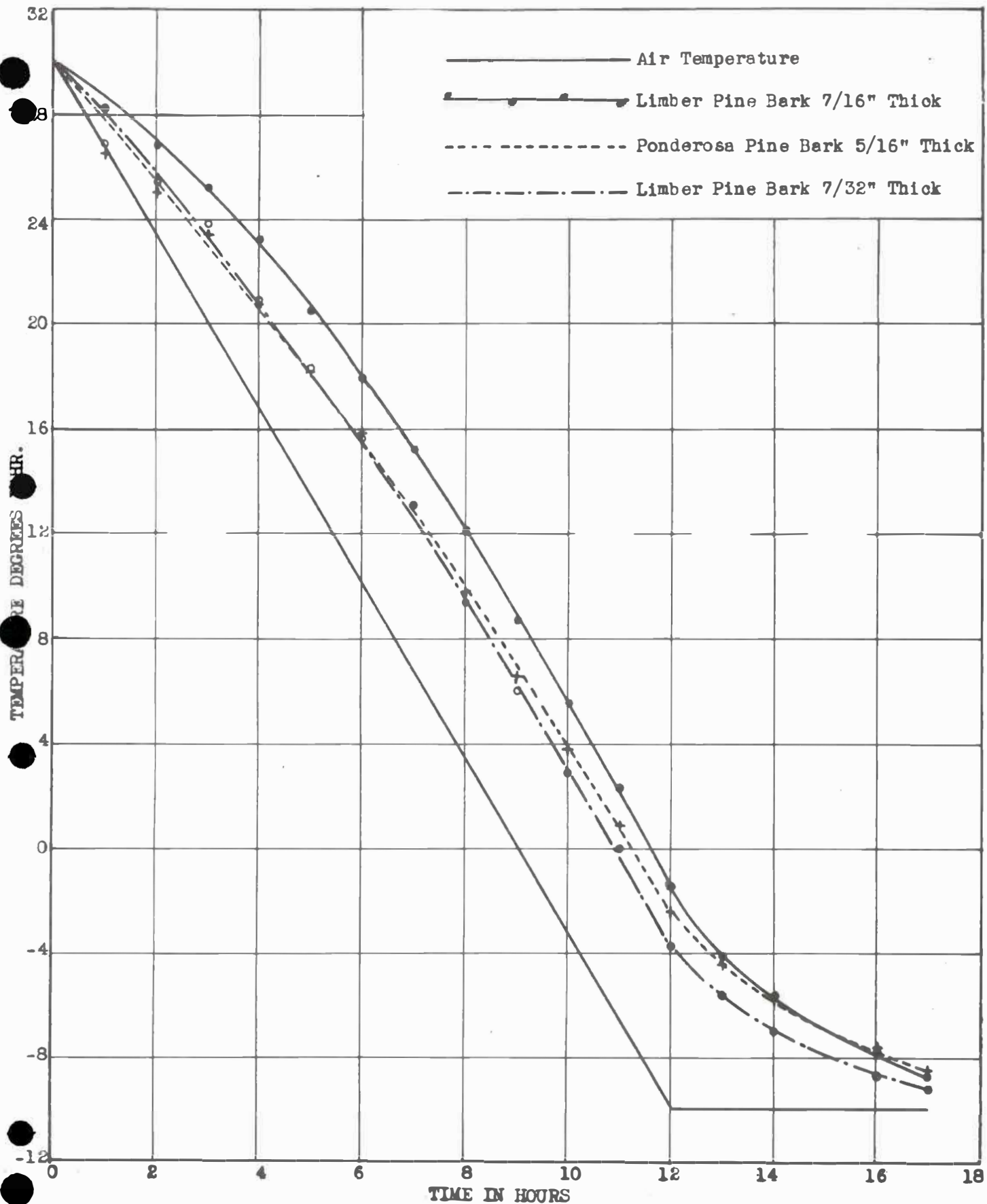


Figure 24. Relation of subcortical temperatures to air temperature during a 40° drop in 12 hours.

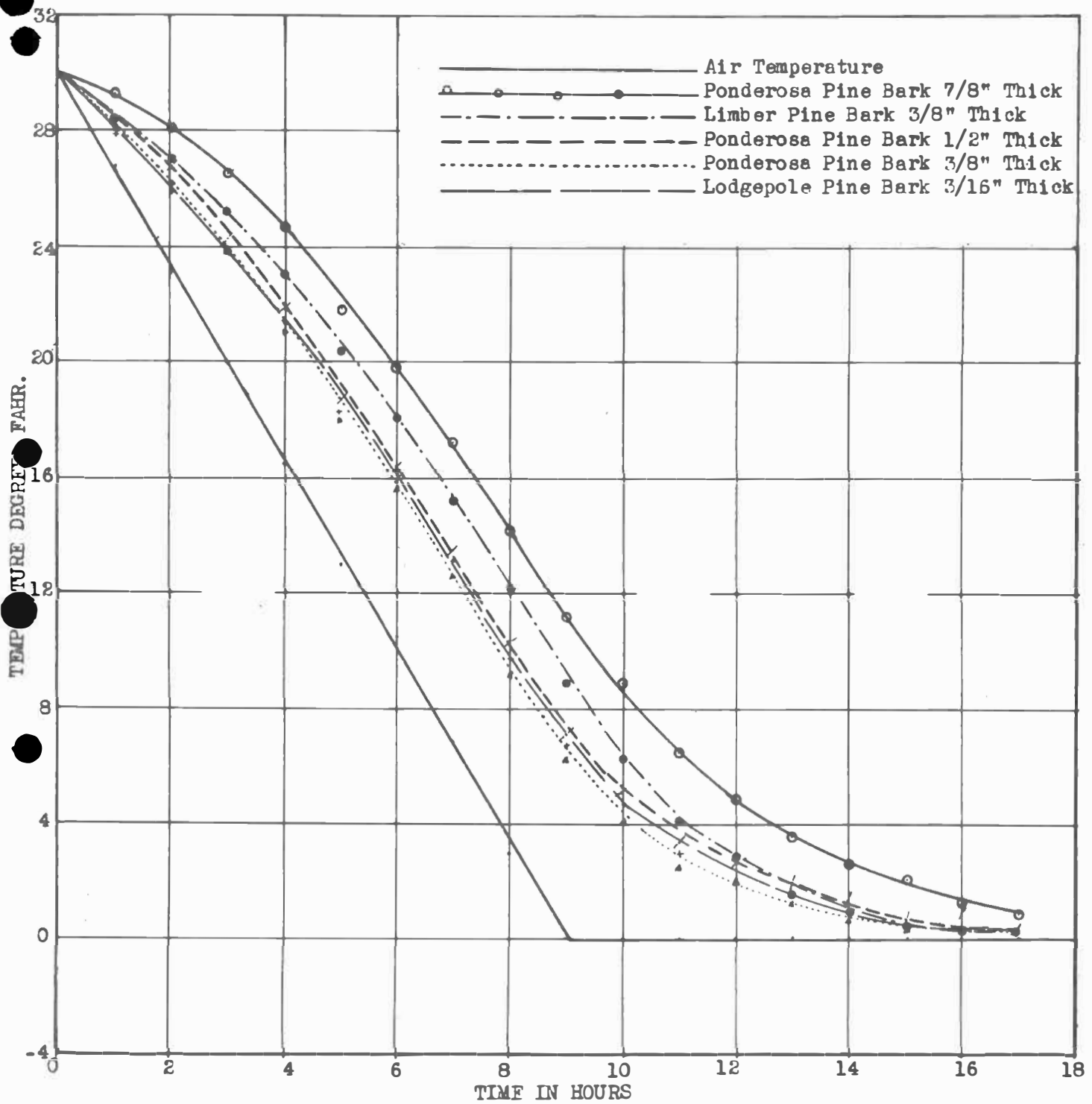


Figure 25. Relation of subcortical temperatures to air temperature during a 30° drop in 9 hours.

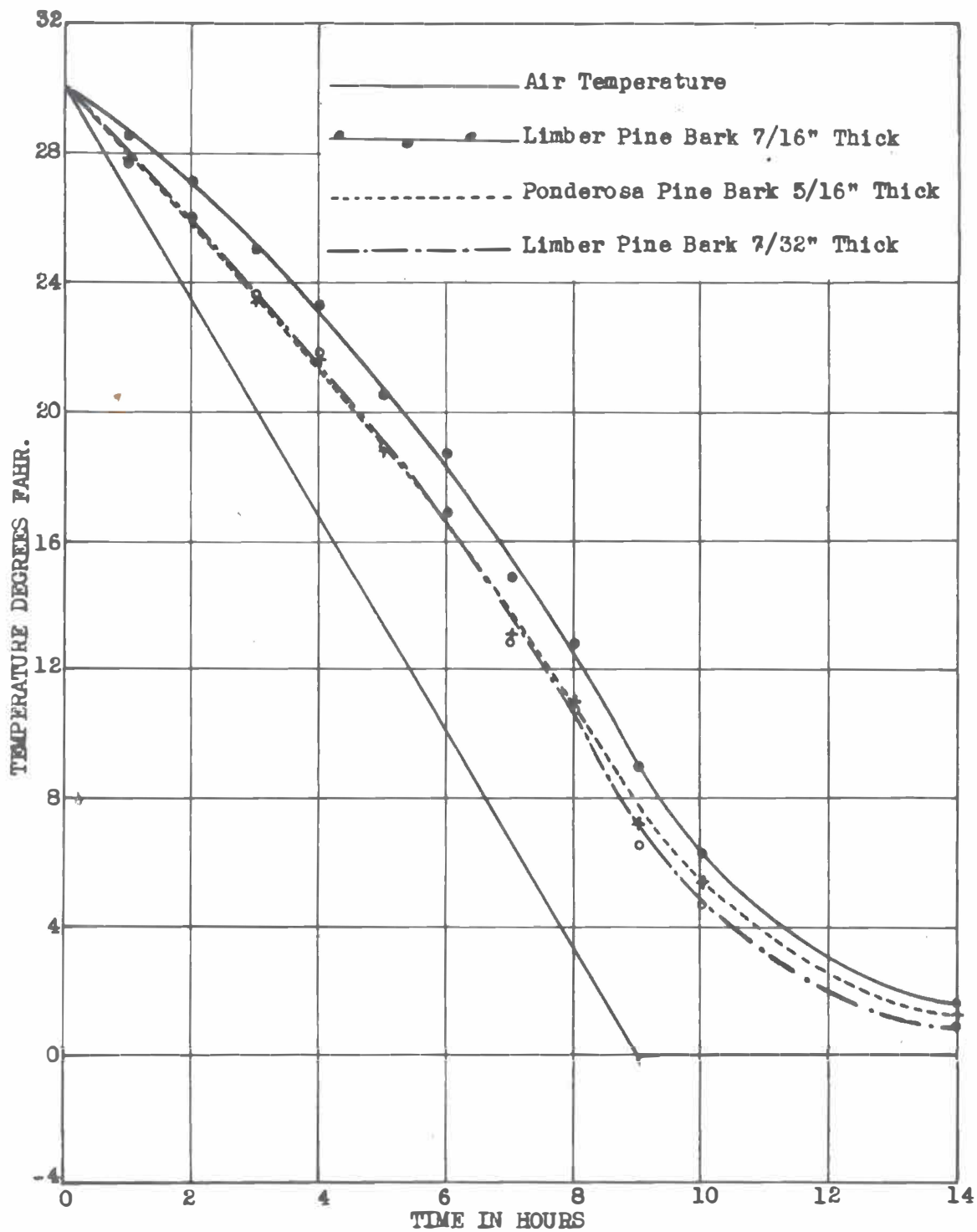


Figure 26. Relation of subcortical temperatures to air temperature during a 30° drop in 9 hours.

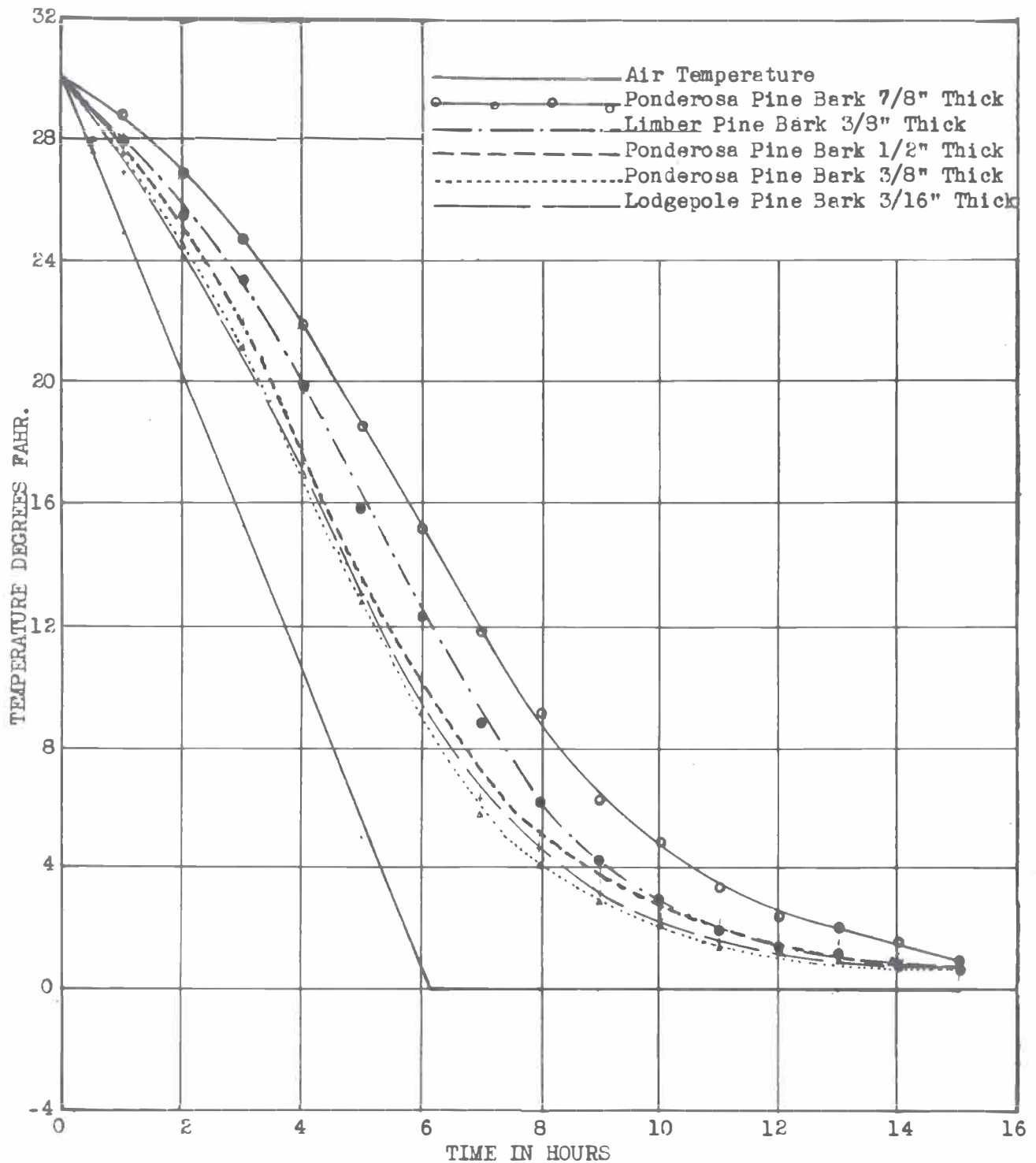


Figure 27. Relation of subcortical temperatures to air temperature during a 30° drop in 6 hours.

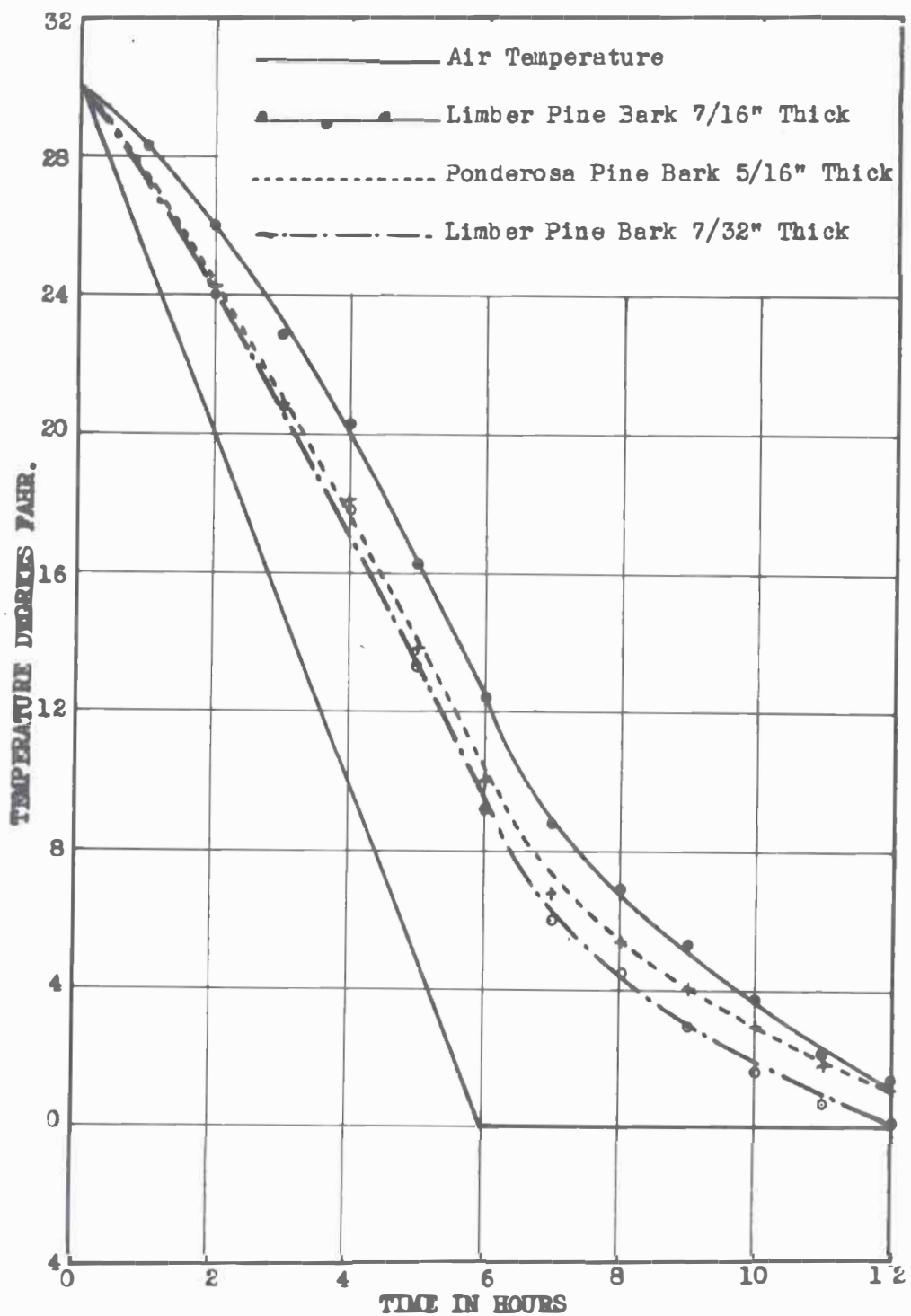


Figure 28. Relation of subcortical temperatures to air temperature during a 30° drop in 6 hours.

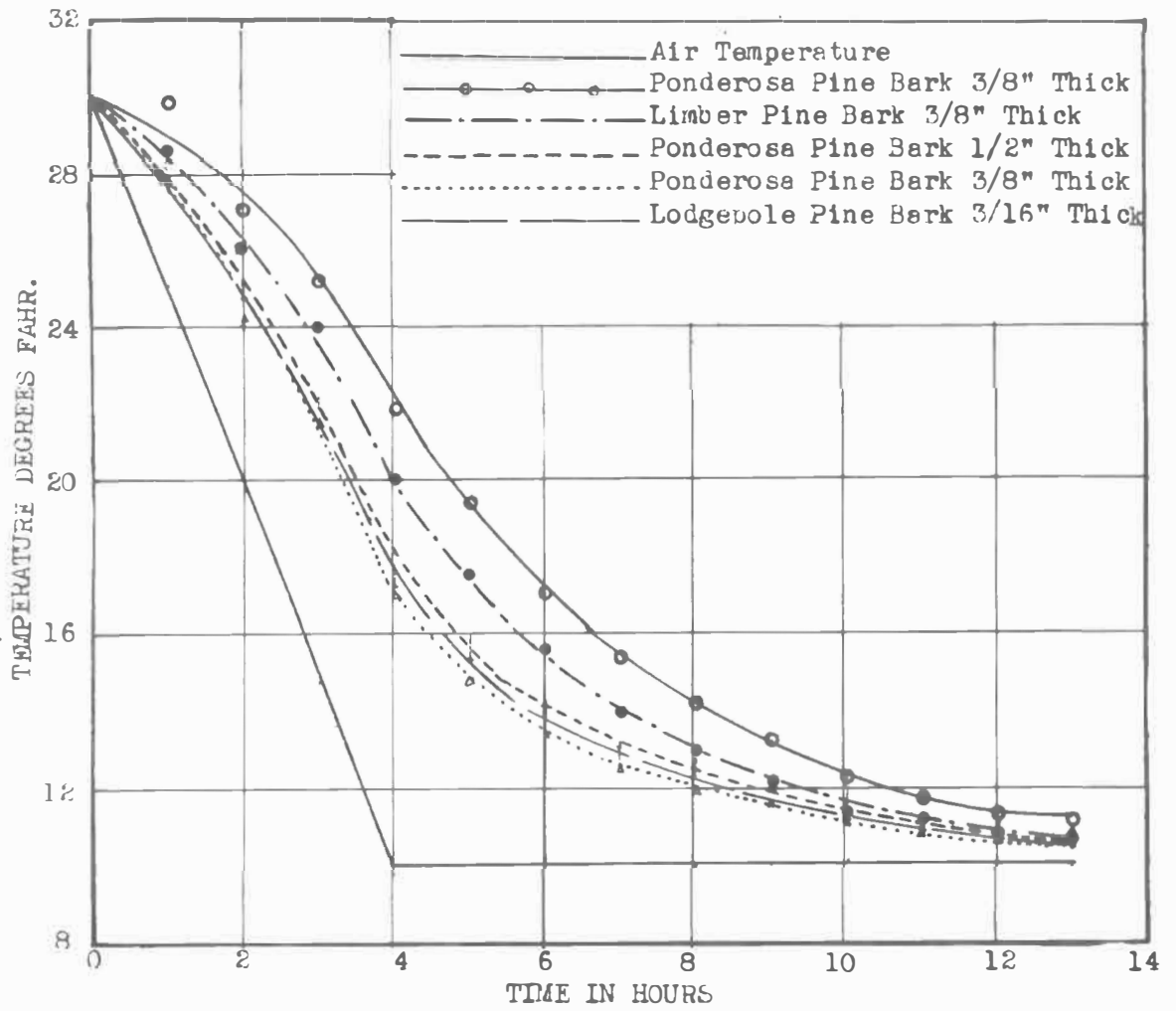


Figure 29. Relation of subcortical temperatures to air temperature during 20° drop in 4 hours.

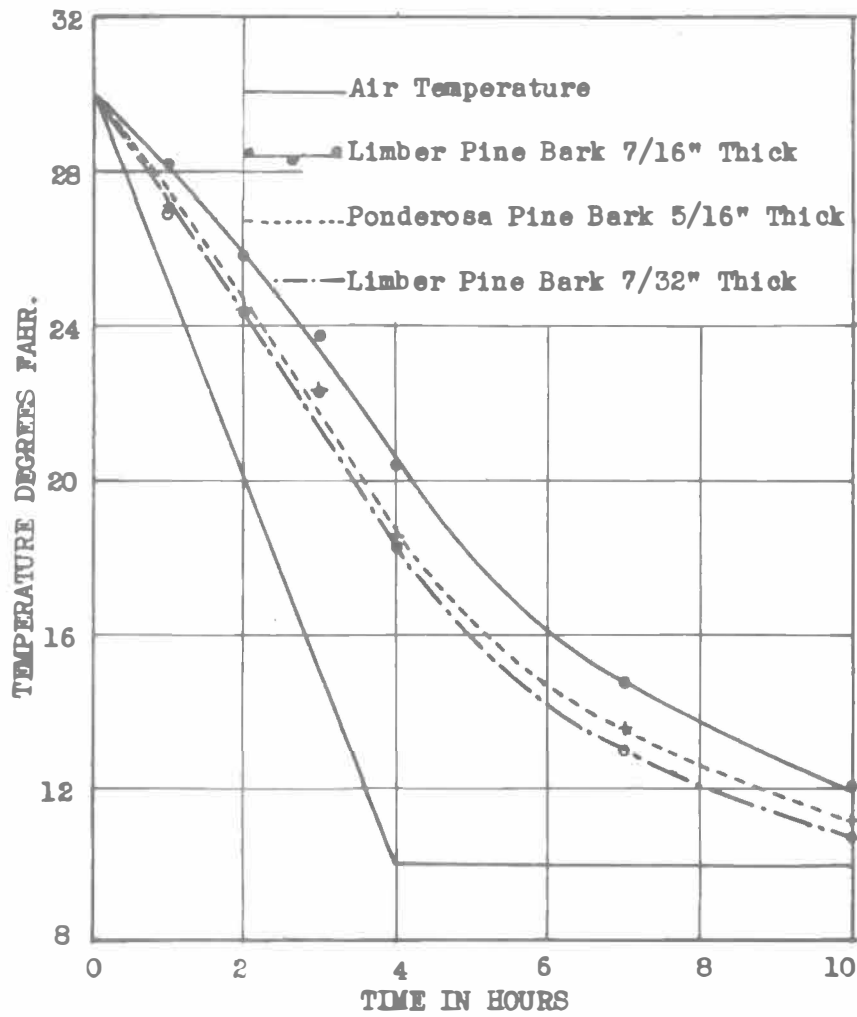


Figure 30. Relation of subcortical temperatures to air temperature during a 20° drop in 4 hours.

Figures 25 and 26 represent the same rate of drop, $3\frac{1}{3}^{\circ}$ per hour, as that in the preceding two figures, but in this case the total drop was 30° in 9 hours. Since the rate of drop was the same the lags were similar.

Figures 27 and 28 show the relation of subcortical temperatures to air temperature during a 30° drop in 6 hours or a decrease at the rate of 5° per hour. Since the rate is greater, the difference between air temperature and subcortical temperatures is also greater.

Figures 29 and 30 show the relation of subcortical temperatures to air temperature during a 20° drop in 4 hours.

The lag of subcortical temperatures behind air temperatures is summarized in Table XIV. The lag of subcortical temperature behind air temperature in bark of like thickness is approximately the same with a drop of 5° per hour as it is with a drop of $3\frac{1}{3}^{\circ}$ per hour. However, the difference between subcortical temperature and air temperature is greater at any given time with the greater rate of decrease.

Table XIV

Relation of Subcortical Temperature to Air Temperature

Bark Thickness in Inches	40° Drop in 12 Hours		50° Drop in 6 Hours	
	Lag of Temperature in Hours	Difference between Air and Subcortical Temperatures	Lag of Temperature in Hours	Difference between Air and Subcortical Temperatures
Ponderosa Pine 7/8	3.5	11.0	3.4	14.4
Ponderosa Pine 1/2	2.2	7.0	1.8	9.4
Ponderosa Pine 3/8	2.0	6.4	1.5	8.2
Ponderosa Pine 5/16	2.2	7.4	2.1	10.4
Limber Pine 7/16	2.7	8.7	2.5	12.5
Limber Pine 3/8	2.8	8.8	2.6	11.8
Limber Pine 7/32	1.8	6.4	1.8	9.4
Lodgepole Pine 3/16	2.1	6.6	1.6	8.6

1. This column shows the lag of subcortical temperatures behind air temperature.

2. This column shows the greatest difference between subcortical and air temperature.

The limber pine bark has a higher insulating value than ponderosa pine bark of equal thickness. This may be explained by the fact that limber pine bark does not have deep crevices similar to the ponderosa pine bark. Likewise the lodgepole pine bark is smoother.

The insulation afforded by bark of the same host species does not always vary directly with bark thickness. The particular sample of 5/16 inch ponderosa pine bark was a better insulator than the thicker 3/8 inch bark. Likewise, the temperature lag under the 3/8 inch limber pine was greater than that under the thicker 7/16 inch bark.

A low of -15° on November 6, 1933 produced a mortality of 29 percent of the larvae in ponderosa pine on the Pike National Forest and a low of -34° on February 6, 1933 produced a 50 percent mortality on the Roosevelt National Forest. Referring to the critical range of ponderosa pine larvae in Figure 16 it is seen that the subcortical temperatures must have been approximately 12° higher than the air temperature to produce the respective mortalities.

WINTER-KILL OF THE BLACK HILLS BEETLE ON THE PIKE NATIONAL FOREST, COLORADO, NOVEMBER 6, 1933

In mid-January 1933, during an inspection of the spotting and control work being done on the Pike National Forest against the Black Hills beetle, considerable winter-kill was noted among some of the larvae. Preliminary examination indicated that the mortality might be sufficiently heavy to permit some changes in control plans. It was therefore decided to make a more detailed examination of the infested areas in order to determine the extent and severity of the winter mortality among the larvae. A crew of 5 men spent 10 days sampling the different areas and during this time 89 infested ponderosa pine trees were felled, 690 samples, 6 by 6 inches, were

Table XV

MORTALITY OF OVERWINTERING LARVAE OF THE BLACK HILLS BEETLE—NORTH AND SOUTH SIDES OF TREES OF ALL AREAS
PINE NATIONAL FOREST

North Side																			
Bark thickness in inches	.2	.3	.4	.5	.6	.7	.8	.9	1.0										
Area	A*	D**	A	D	A	D	A	D	A	D	A	D	A	D	A	D	A	D	dead
Upper Deer Crk.	14:	31:	20:	107:	68:	61:	106:	185:	259:	147:	226:	97:	574:	47:	156:	0:	238:	18:	27
Estabrook	—:	—:	—:	—:	115:	26:	448:	335:	310:	76:	344:	37:	98:	8:	127:	0:	207:	18:	25
Shawnee	—:	—:	10:	1:	219:	121:	190:	198:	531:	84:	428:	57:	131:	18:	408:	33:	232:	23:	21
Bailey	—:	—:	32:	2:	—:	28:	451:	231:	151:	62:	193:	15:	89:	2:	13:	0:	74:	3:	23
Cheesman Lake	—:	—:	203:	134:	270:	306:	553:	236:	487:	239:	431:	230:	573:	91:	262:	53:	415:	35:	27
Totals	14:	31:	265:	244:	730:	442:	1733:	1126:	1563:	608:	1677:	406:	1315:	153:	966:	91:	1164:	97:	26
% mortality		69:		43:		36:		41:		26:		23:		11:		9:		8:	

South Side																			
Upper Deer Crk.	—:	—:	5:	107:	54:	115:	60:	376:	215:	187:	184:	153:	198:	45:	123:	3:	632:	30:	40
Estabrook	—:	—:	0:	4:	220:	112:	128:	103:	378:	256:	139:	34:	152:	13:	117:	0:	94:	2:	30
Shawnee	48:	22:	3:	0:	60:	25:	233:	241:	476:	370:	23:	13:	224:	50:	101:	10:	207:	49:	35
Bailey	—:	—:	—:	—:	67:	19:	135:	45:	228:	81:	250:	105:	24:	79:	—:	—:	272:	14:	24
Cheesman Lake	9:	13:	63:	155:	136:	140:	495:	516:	521:	253:	681:	237:	416:	25:	395:	45:	329:	30:	51
Totals	57:	35:	71:	266:	547:	411:	1049:	1086:	1321:	1252:	1360:	545:	1014:	167:	639:	58:	1534:	125:	33
% mortality		38:		79:		45:		51:		41:		29:		14:		8:		7:	
% mortality																			
North & south		48:		60:		40:		45:		35:		25:		12:		8:		7:	
North & south																			
Total mortality:																			29

* A = live larvae

** D = dead larvae

taken, and 84,926 larvae observed for mortality. Samples were taken on both north and south sides of the trees at intervals of 5 feet from the lowest to the highest point of infestation. The number of dead and living larvae were recorded and measurements taken of the bark thickness and diameter of trees at each sample as well as height of sample on tree, aspect, and location.

The only lethal low temperature as shown by the weather records at Cheesman Lake and Bailey, Colo. (the only two official weather stations in the area) occurred on November 6, 1938 when the minima were -5° and -15° respectively. Critical low temperature studies of the Black Hills beetle larvae in the laboratory at Fort Collins show that -5° would kill approximately 50 percent and -15° 100 percent (when not protected by the bark) at that time of the year (Figure 16).

The data on the counts are tabulated in Table XV according to side of tree, area, and bark thickness. The mortality varied considerably not only by areas but also according to bark thickness and side of tree. Total mortality from the north side of all trees sampled varied from 69 percent in thin bark to 8 percent in the thicker bark and averaged 26 percent. From the south side it varied from 60 to 7 percent and averaged 33 percent. The average mortality from both sides was 29 percent. The relation of the winter mortality to bark thickness and side of tree is shown in Figure 31. The higher mortality found on the south side of the trees is attributed

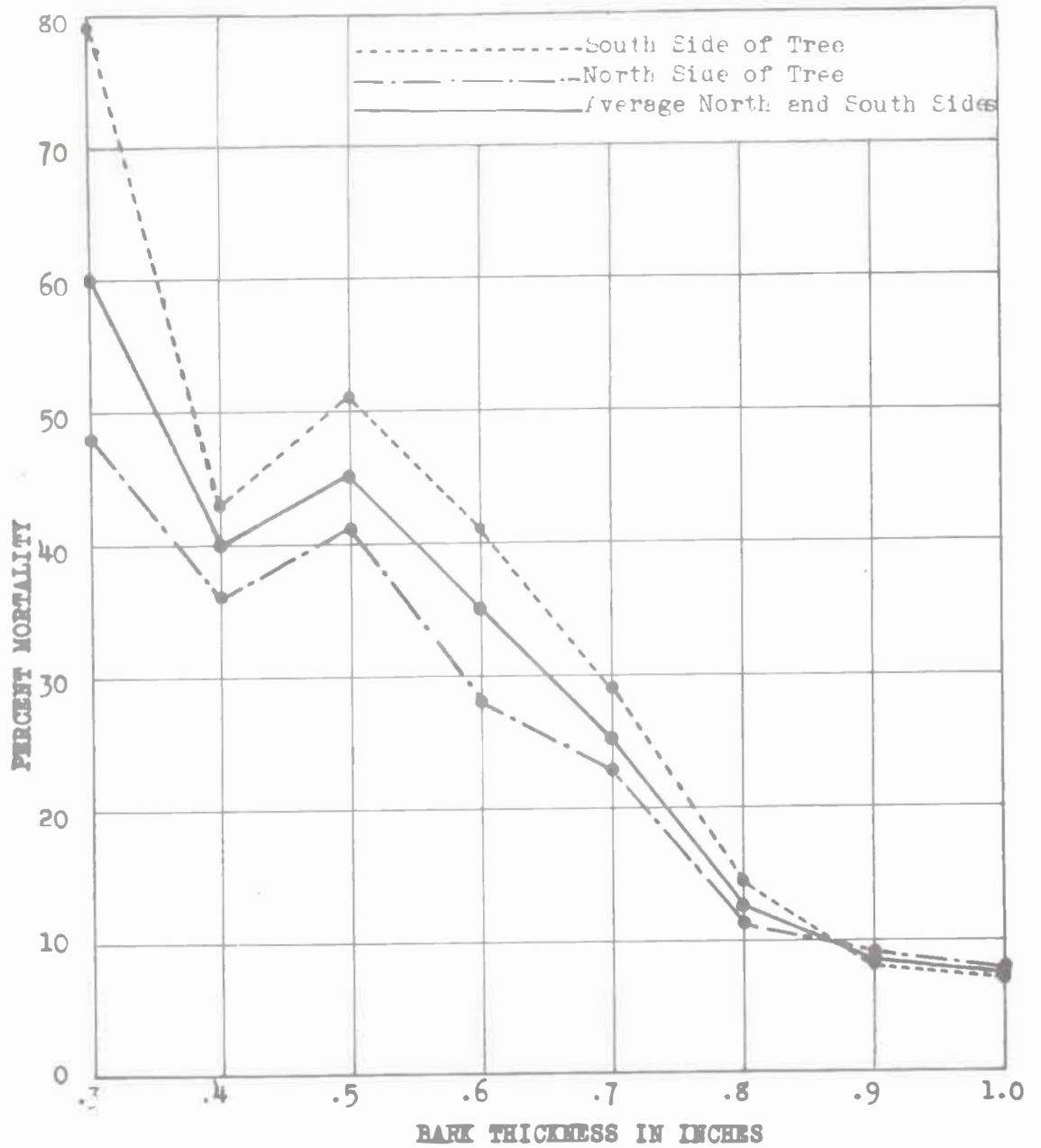


Figure 31. Relation of winter mortality to bark thickness.

to the fact that the cold hardness of the larvae had advanced less on that side than on the north side. In general, winter-kill was heaviest under the thinner bark. In cases where this was not true, such as under bark 0.2 inch in thickness, the number of samples was inadequate. Under bark 0.4 inch in thickness the mortality does not fall in line, probably because many of the thinner bark samples were taken from large, over-mature, smooth-barked trees with shallow bark crevices which offer more insulation, while many of the others were taken from very irregular bark on younger and faster growing trees with deep crevices.

The percent mortality of the larvae is given by areas and by bark thickness in Table XVI. The winter kill was not complete in any area nor under the thinnest bark measured. Although no counts were made under the bark of limbs, it was estimated that the mortality approached 100 percent. Mortality in the trunks of the trees in different areas varied from as high as 40 percent to as low as 10 percent, and it should be noted that these occurred in the south end of Lake George and the north end of Lake George, respectively, where only rough estimates were made. In other areas it varied from 23 percent in the Bailey area to 36 percent in the Shawnee area, two closely associated localities. The other areas and the mortality ratings are: Deer Creek with 36 percent, Estabrook with 27 percent, and Cheesman Lake with 29 percent. Mortality for all areas based on the total number of larvae was 29 percent. The samples were distributed

Table XVI

PERCENT MORTALITY OF OVERWINTERING LARVAE OF THE BLACK HILLS BEETLE
ON THE PIKE NATIONAL FOREST

Area	No. of trees	No. of samples	Bark thickness in inches and percent mortality									
			.2	.3	.4	.5	.6	.7	.8	.9	1.0	Total mortality
Upper Deer Creek	13	112	69	90	57	77	41	34	13	1	5	36
Estabrook	10	98	--	100	29	44	83	20	5	0	0	27
Shawnee	15	133	31	7	34	32	36	12	14	9	14	38
Bailey	7	54	--	6	20	32	26	21	27	0	5	25
Cheesman Lake	23	225	60	52	46	35	37	29	10	15	8	29
North end Lake George	11	43	20	15	23	5	5	0	--	--	0	10
South end Lake George	10	15	--	65	35	50	45	30	0	--	--	40
Average*	89	680	49	60	40	45	35	25	12	9	7	29

*Weighted average exclusive of Lake George areas where estimates rather than actual counts were made.

in bark of trees typical of the area and the estimate should be accurate for the whole forest.

WINTER-KILL ON ROOSEVELT NATIONAL FOREST
WINTER 1932-33

An examination of the Black Hills beetle infestation on the Roosevelt National Forest by Baumhofer, in company with Forest Service officials April 3-6, 1933, revealed that there was a heavy mortality of the overwintering brood. An unpublished memorandum was prepared by Baumhofer (1933) in which he states: "Considerable brood mortality was found in most of the infested trees and it was roughly estimated that this mortality would average nearly 50 percent. It is possible that two periods of extremely low temperatures during the past winter were a factor in causing this mortality."

An examination of the weather records at Estes Park, Colo., which is in the ponderosa pine type, and approximately the same elevation as the areas examined by Baumhofer, reveals that there were two periods of extremely low temperatures during that winter. On December 12, 1932 a temperature of -20° was recorded and on February 8, 1933 a temperature of -34° . Since the larvae from ponderosa pine are as cold-hardy in December as in February and winter temperatures as low as -20° are not uncommon, it is reasonable to assume that the low of -34° on February 8 caused the mortality. A temperature as low as that is sufficient to kill all the larvae when not protected by the bark.

FREQUENCY OF LETHAL LOW TEMPERATURES IN THE FIELD

Two cases of the lethal effects to overwintering larvae of the Black Hills beetle have already been mentioned. To determine the frequency of minimum temperatures sufficiently low to produce mortality, the weather records of several weather stations were examined. The number of weather stations located so as to be applicable to forested areas subject to attack by the Black Hills beetle are very limited. The weather stations are usually located in the larger cities, which are in turn located at lower elevations or in valleys and the records are not applicable.

Minimum Temperatures in Ponderosa Pine Type

Fortunately there were several official Weather Bureau stations located in the ponderosa pine type on the eastern slope of the Continental Divide, where a number of epidemics have occurred. The stations are all within or near the boundaries of the Roosevelt and Pike National Forest. The stations and a brief description of each are as follows:

Estes Park, Colo., Larimer County, elevation 8,000 feet, country mountainous and forested, no water in vicinity, station located 4 miles west-northwest of Estes Park Post Office, 1916 to 1939.

Rugh's Ranch, Colo., Larimer County, elevation 7,150 feet,

station located on hay ranch in Poudre River valley, 1909 to 1929.

Cheesman Lake, Colo., Jefferson County, elevation 8,390 feet, hilly and mountainous, station about 40 feet above and 100 feet distant from shore of lake, forest growth on hillsides, 1903 to 1939.

Elk Creek, Colo., Park County, elevation 8,144 feet, station over sod ground under big pine tree, 100 feet from Black Mountain Creek and 500 feet from Elk Creek, open park or valley, mountainous, 1919 to 1933.

Longs Peak Inn, Colo., Larimer County, elevation 8,956, mountainous, station in park at foot of Longs Peak, 1896-1939.

Monument, Colo., El Paso County, elevation 7,200 feet, rolling country, station is at base and 1 mile east of Mount Herman which rises 2,000 feet above, 1911 to 1939.

The minimum temperature during each 5-day period of each month was tabulated from September to April inclusive. The last period of each month with 31 days included 6 days and the last period of February included 3 or 4 days. From these tables the record minimum for each 5-day period was determined during the period records were available. These minimum temperatures were then charted with the critical low temperature range of larvae from ponderosa pine. These data are shown in Figures 32-34. Because of the insulating values of bark already mentioned the temperature must reach below

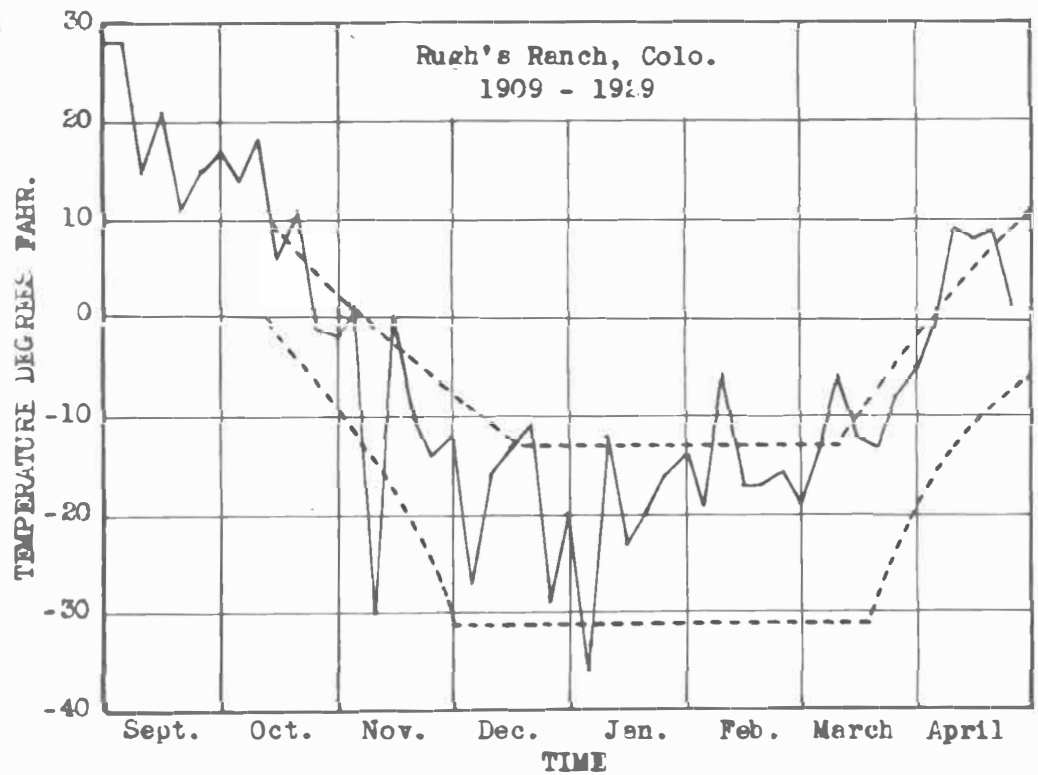
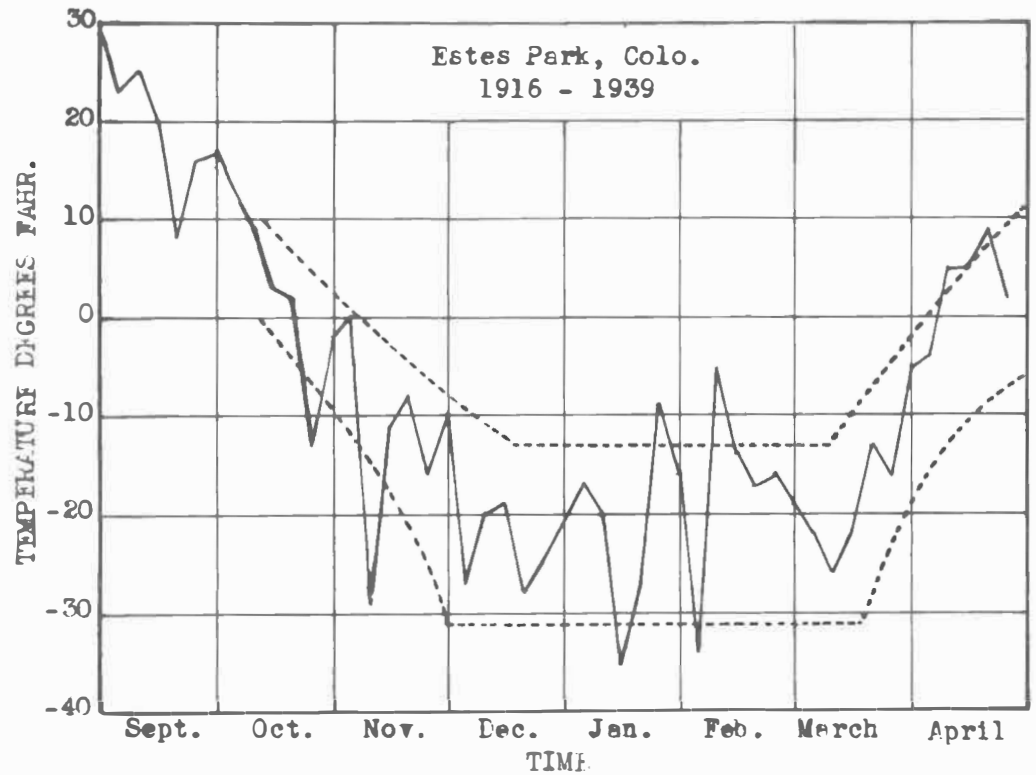


Figure 32. Minimum temperatures and critical range of Black Hills beetle larvae from ponderosa pine.

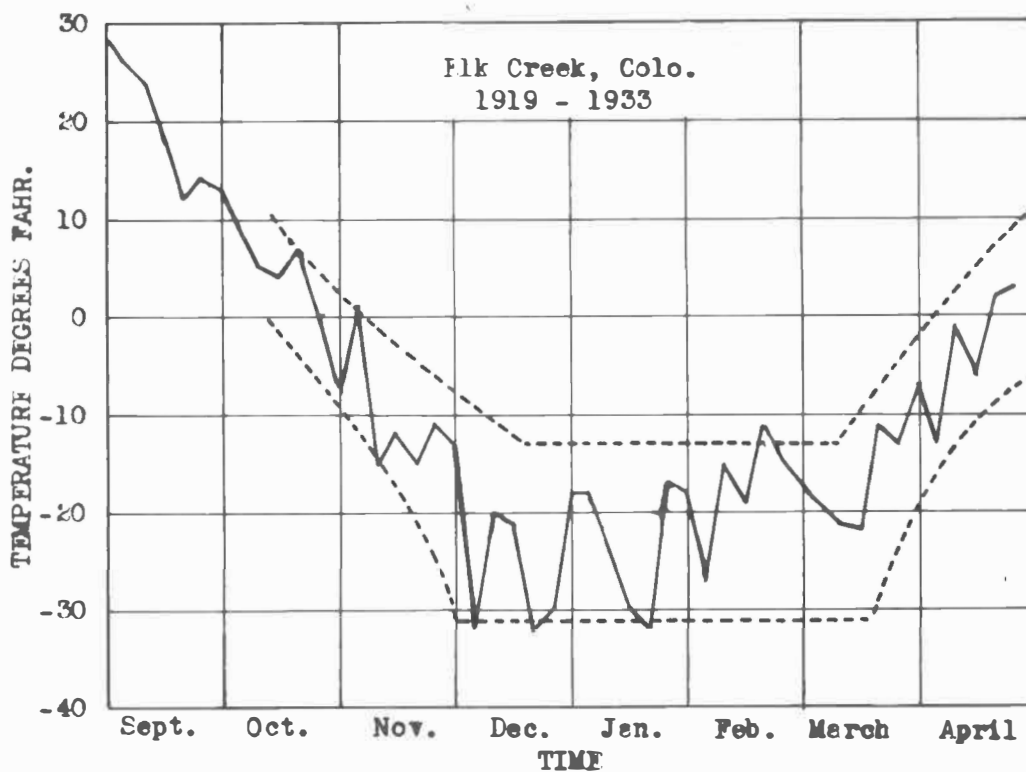
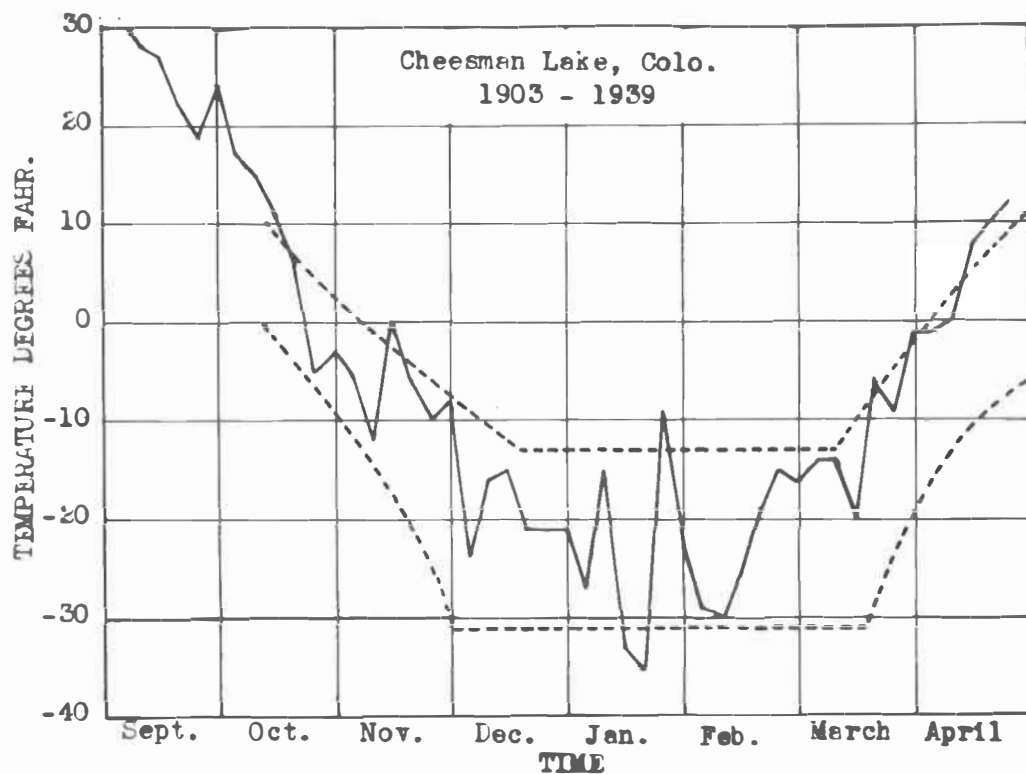


Figure 33. Minimum temperatures and critical range of Black Hills beetle larvae from ponderosa pine.

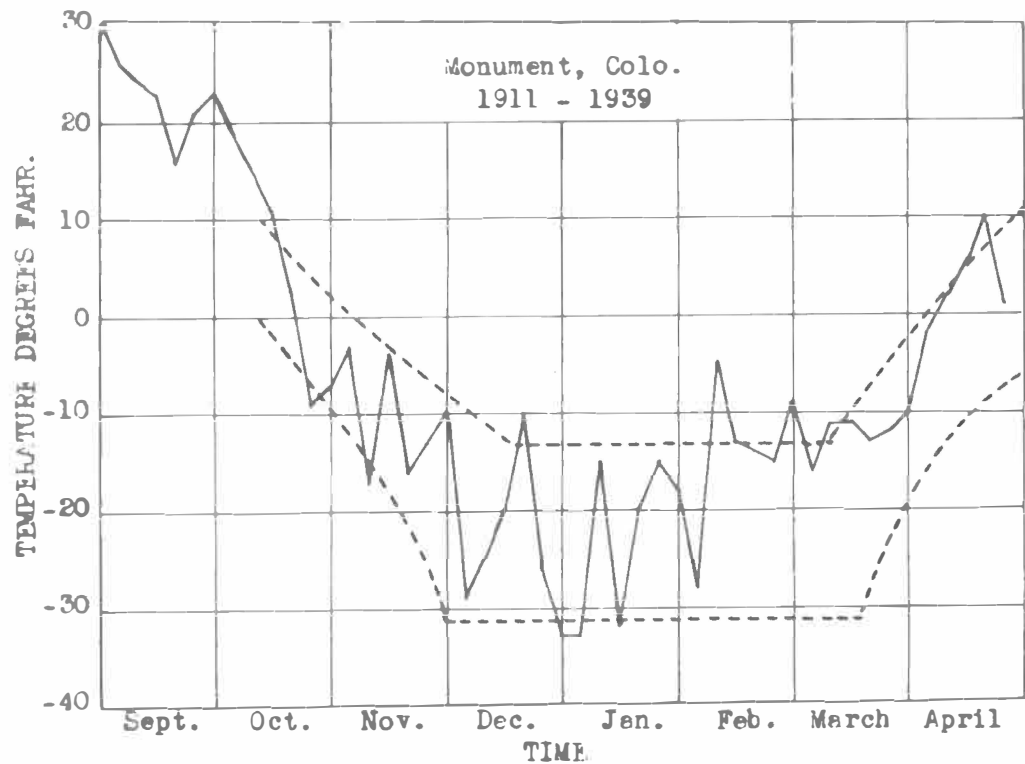
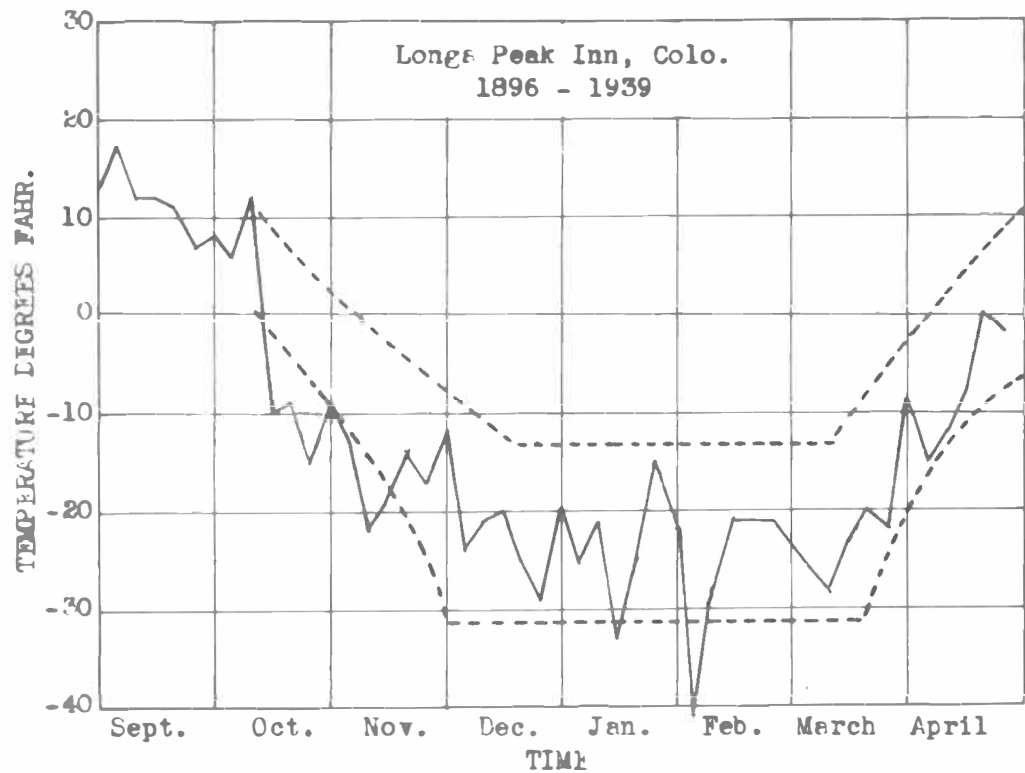


Figure 74. Minimum temperatures and critical range of Black Hills beetle larvae from ponderosa pine.

the 100 percent mortality range for naked larvae to produce significant mortality under the bark. This is substantiated by two known winter kills that occurred in the field relatively near official weather stations. The first one occurred on February 3, 1933 on the Roosevelt National Forest when a temperature of -34° was recorded at Estes Park, Colorado. This low temperature, which resulted in an estimated mortality of 50 percent, is approximately 3° lower than the ultimate critical range of larvae from ponderosa pine. The second one, during which a 29 percent mortality resulted, occurred on November 6, 1933 on the Pike National Forest when a temperature of -15° was recorded. This low temperature was approximately 3° lower than the ultimate critical range of naked larvae from ponderosa pine.

In the discussion that follows low temperatures other than those mentioned as producing a significant amount of mortality undoubtedly produced a small amount of mortality, at least under the thin bark.

At Estes Park, Colo., 4 low temperatures sufficient to kill brood were recorded (Figure 32). Two of these lows--the first of -15° occurred during October 26-31, 1917, and the second of -29° occurred during November 11-15, 1916--were unseasonable and should have produced heavy mortality because the larvae probably had not reached maximum hardiness at that time of the year. The other two

lows of -35° during January 16-20, 1930 and -34° during February 6-10, 1933 occurred during maximum hardness of the larvae. The last mentioned low was probably responsible for a 50-percent mortality of the brood as reported by Baumhofer and already mentioned.

At Rugh's Ranch, 1909-1929, two probably lethal temperatures occurred (Figure 32). The first of -30° was unseasonable and occurred during November 11-15, 1916 the same time the low was recorded at Estes Park. The second of -33° occurred during January 6-10, 1913 before records were taken at Estes Park.

The station at Cheesman Lake, Colo. is probably at too low an elevation to be applicable to the forest that lies somewhat above it. Two low temperatures of -33° and -35° were recorded during one cold wave January 16-25, 1930 (Figure 33). A known mortality of 29 percent occurred following a low of -5° recorded at this station on November 6, 1930 which indicates that the temperatures from this station are not applicable. During this same coldwave a temperature of -15° was recorded at Bailey, Colo. a short distance away and at a higher elevation.

The Elk Creek, Colo. station was well located but the records ran for only 15 years, 1919-1933. During this time 5 low temperatures occurred that probably killed a small amount of brood, probably less than 30 percent (Figure 33). The temperatures and the dates of occurrence are as follows: -8° , November 1-5, 1929; -15° , November

11-15, 1925; -13° , December 6-10, 1919; -32° , December 26-31, 1924; and -33° , January 21-25, 1930. There were several other midwinter lows of -30° which may also have produced a small amount of mortality.

The station at Longs Peak Inn, Colo. is probably at too high an elevation to be applicable to the ponderosa pine type but is included to show the relation of minimum temperatures at the higher elevations and the lower elevations. Actually the minimum temperatures at the higher elevations are not necessarily lower than those at the lower elevations. Sometimes cold waves that strike the lower plains country never hit the higher mountainous country and vice versa. The records in Figure 34 indicate that there are a number of October and November minimum temperatures that would be fatal. Under actual conditions at this altitude the larvae would start their cold conditioning earlier in the fall and reach the maximum cold resistance in November instead of December. The average fall temperatures at this station are lower and this would initiate cold hardening at an earlier date. There was one low of -41° recorded during February 6-10, 1933 that probably should have produced mortality.

The records at Monument, Colo. indicate that lethal temperatures occurred on 5 occasions 1911-1939 (Figure 34). The temperatures and the dates of their occurrence are as follows: -9° , October 26-31, 1911; -17° , November 11-15, 1936; -33° , January 1-5, 1911; -35° , January 6-10, 1913; and -32° , January 16-20, 1930. None of these

temperatures were probably low enough to produce a high percentage of mortality.

Eighteen lethal low temperatures have occurred, during the total of 126 years' records at 5 weather stations (excluding Longs Peak Inn) in the ponderosa pine type. These fatal temperatures occurred during the fall and winter and never in the spring.

Minimum Temperatures in Limber and Lodgepole Pine Types

Limber and lodgepole pine occurs at higher elevations than ponderosa pine. Since the critical ranges of larvae from limber and lodgepole pine were determined from logs stored at 8,000 feet, the ranges would probably be different if allowed to remain at their natural elevations and climate. In the limber and lodgepole pine types colder weather occurs earlier in the fall and the hardening process would also start earlier. For this reason some of the October and November temperatures that appear to be fatal on the charts actually would not be fatal under natural conditions.

The official Weather Bureau Stations in this type are very limited. The stations and a brief description of each are as follows:

Fox Park, Wyo., Albany County, Medicine Bow National Forest, elevation 9,015 feet, station in standing timber, 1910-1939.

Centennial, Wyo., Albany County, elevation 8,074 feet, station located in small valley at the foot of the Medicine Bow Mountains to the westward, 1911-1939.

Fraser, Colo., Grand County, Arapaho National Forest, elevation 8,560 feet, station located in rolling mountainous valley, no forests or bodies of water in vicinity, 1910-1939.

Lake Moraine, Colo., El Paso County, Pike National Forest, elevation 10,152 feet, mountainous, station 200 feet from shore of Lake Moraine, forests 1/2 mile away, 1894-1939.

Dome Lake, Wyo., Johnson County, Bighorn National Forest, elevation 8,320 feet, station on west slope of rock ledge in valley surrounded by mountains rising 2,000 feet higher, trees 25 feet away, 1909-1939.

Hunter's Station, Wyo., Johnson County, Bighorn National Forest, elevation 7,400 feet, station in small valley that drains southeastward, on east slope of mountains, heavy timber 40 yards southeastward and westward, lighter timber eastward, 1906-1939.

The minimum temperatures during the 5-day periods at each of the above stations are shown in Figures 35-37.

Figure 35 gives the minimum temperatures at Fox Park and Centennial, Wyo. on the Medicine Bow National Forest. At Fox Park one very cold temperature of -52° occurred during January 6-10, 1913 which probably killed a high percentage of brood in both limber and lodgepole pine. This cold period must have been local because the minimum recorded on the same date at Centennial, which is also on the Medicine Bow National Forest, was -31° . Sometimes, however,

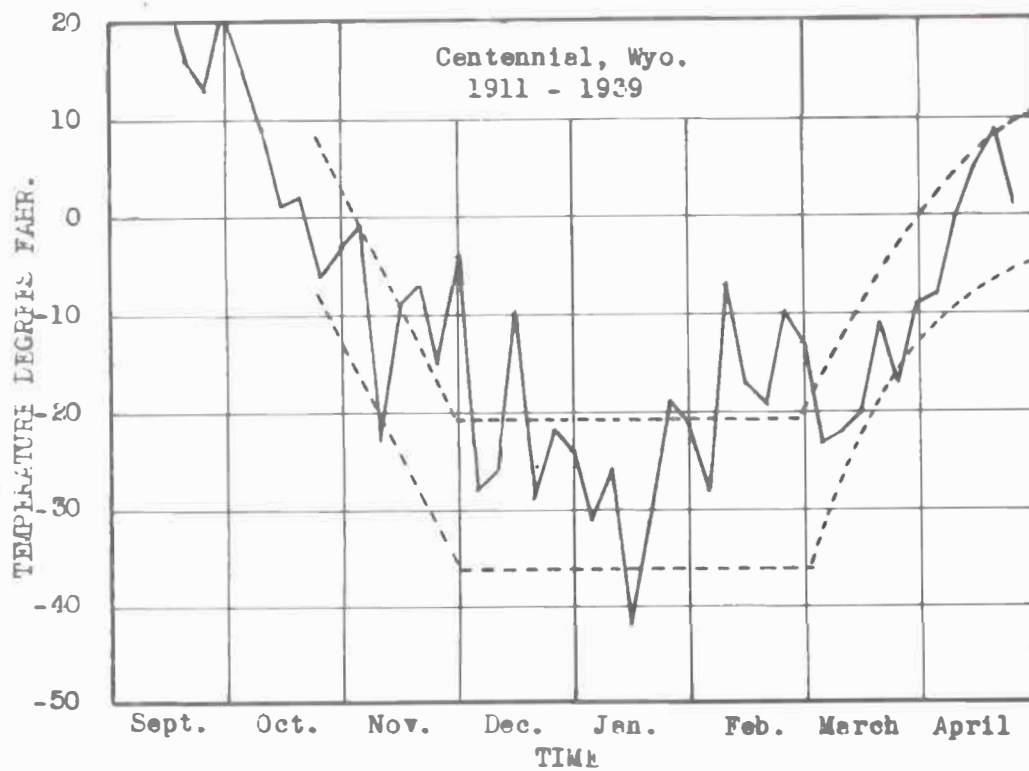
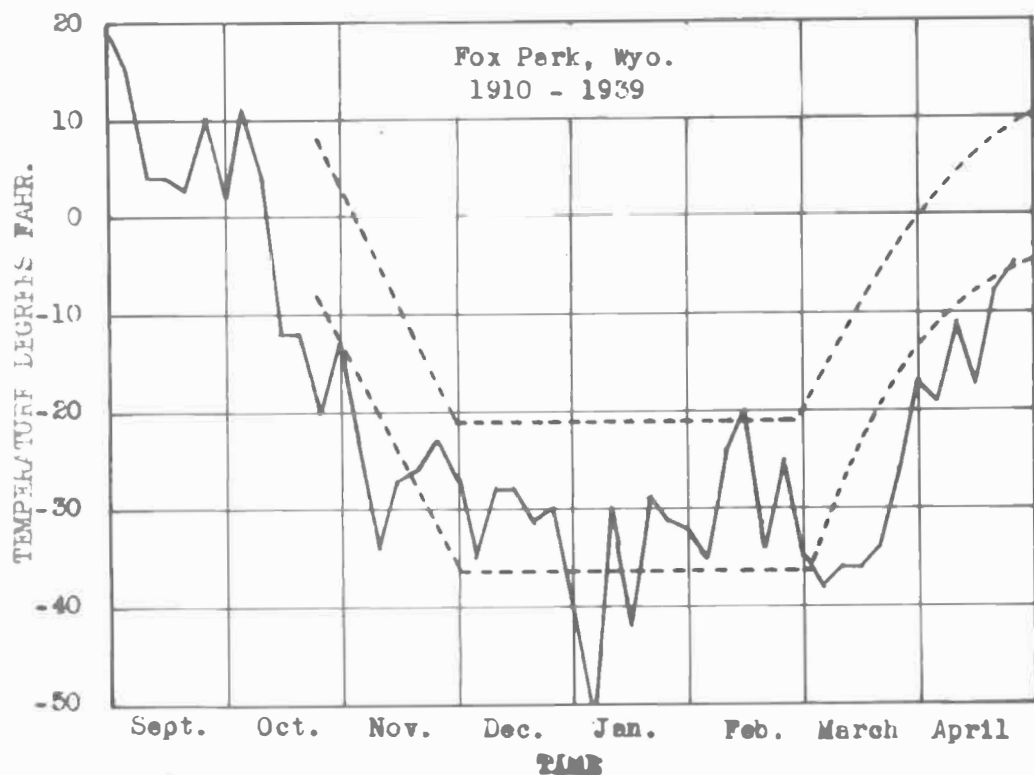


Figure 35. Minimum temperatures and critical range of larvae from lodgepole pine.

the cold waves are more general and similar temperatures are recorded at all stations. One midwinter temperature of -42° , January 16-20, 1930 was recorded at both Fox Park and Centennial.

The minimum temperatures at Fraser, Colo. on the western slope of the Continental Divide were charted (Figure 36) because it seems to be an unusually cold spot. The station is situated in an open valley and the temperatures recorded are probably not applicable to the surrounding forested area.

Lake Moraine, Colo. was chosen as one of the stations because it is one of the few stations located at such a high altitude, 10,265 feet, in the Rocky Mountains and illustrates the fact that minimum temperatures at high elevations are not necessarily lower than those at the lower elevation. The minimum temperatures, for example, at Fraser, Colo. at an elevation of 8,560 feet are much lower than those at Lake Moraine. During the 46 years of records at Lake Moraine there does not appear to have been a lethal low temperature.

The minimum temperatures for Dome Lake and Hunter's Station, Wyo. with the critical range of larvae from limber pine are shown in Figure 37. Both of these stations are in the Bighorn Mountains where an infestation in limber pine has occurred. Low temperatures recorded at these stations do not appear to be lethal. Because of earlier falls and later springs the hardening of the larvae would start earlier in the fall and the decrease in hardness would occur later in the spring than shown in the charts.

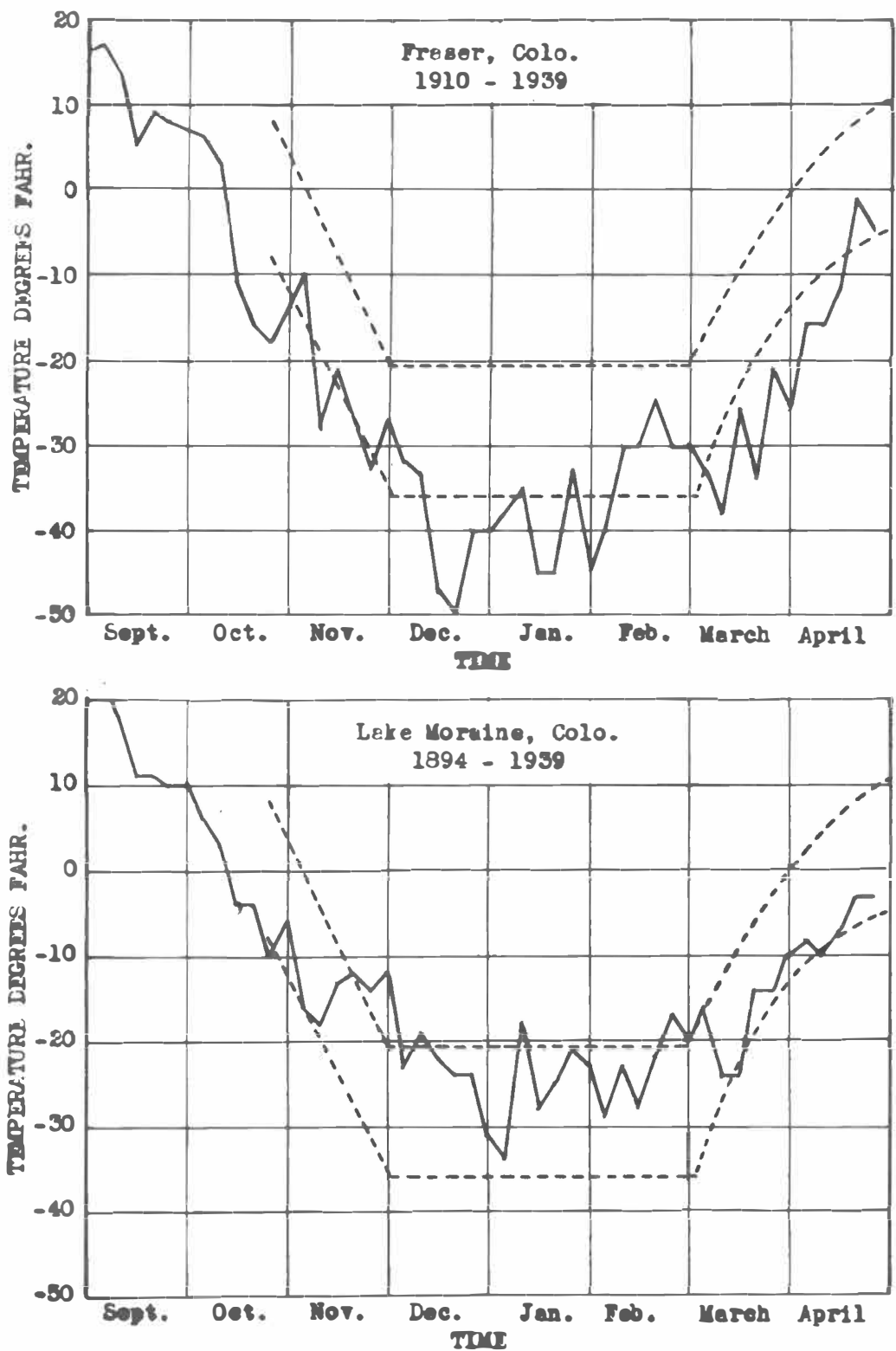


Figure 36. Minimum temperatures and critical range of larvae from lodgepole pine.

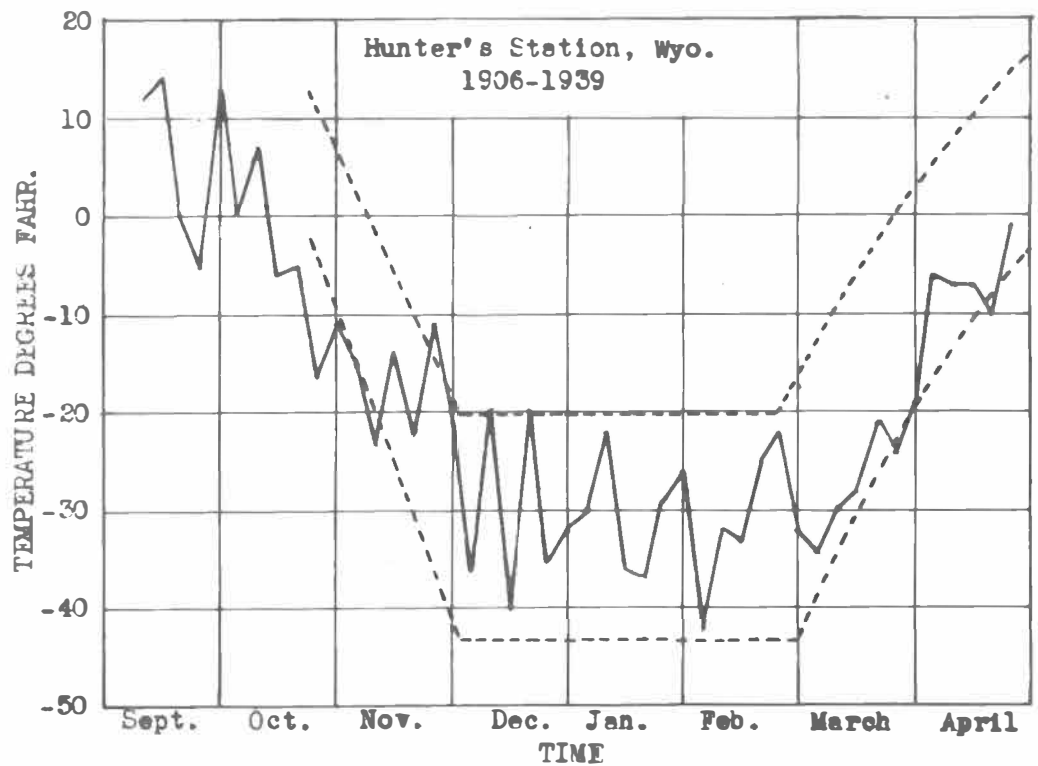
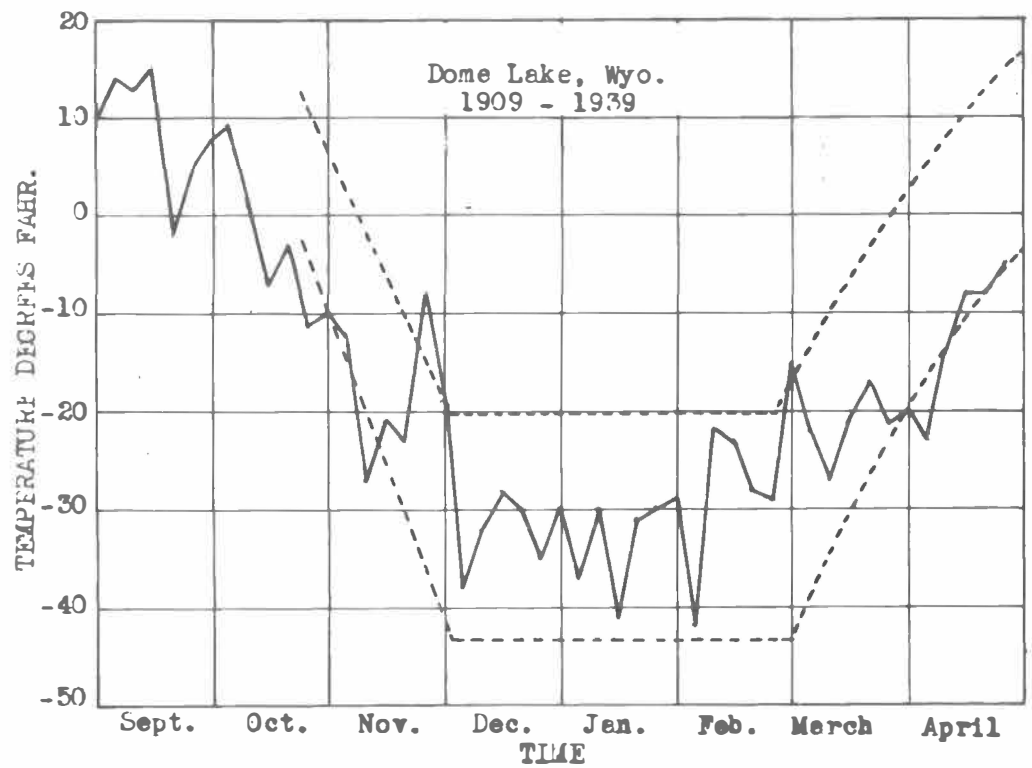


Figure 37. Minimum temperatures and critical range of larvae from limber pine.

SUMMARY

Low winter temperatures are often an important limiting factor of insect distribution and population. Low temperatures have been known to reduce the population of the southern pine beetle and the western pine beetle which are close relatives of the Black Hills beetle. (This study was undertaken to determine the effects of low winter temperatures upon the Black Hills beetle and its relation to the occurrence of serious epidemics.)

The most recent theory as to the cause of death of insects by low temperature is that a high degree of water crystallization causes denaturation and dehydration of proteins. Insects of the ecological group that survive exposures to cold weather are able to increase in cold-hardiness in the fall. Aquatic insects and stored product insects are unable to increase their hardiness and therefore cannot survive low temperatures.

The experiments with the Black Hills beetle were carried out in an automatically controlled well-type, low temperature cabinet with a range of -40° to $+40^{\circ}$. Larvae from ponderosa, limber, and lodgepole pine were removed, for the tests, from infested logs stored in the mountains west of Fort Collins at an elevation of approximately 8,000 feet. The larvae were exposed in petri dishes with 50 paraffin cells, one larva in each cell, for 2 hours and 15 minutes at each $2\frac{1}{2}^{\circ}$ interval over the critical range. During October, November, April, May, and June survival after exposure to the cold was determined by

noting activity. During December, January, and February it was necessary to place each larva in a 2 x 36 mm. vial filled with fresh pine phloem and stoppered with cotton to determine mortality by their ability to feed and develop. During this time of the year a certain percent of the larvae were motile after warming to room temperature even though they were frozen solid during exposure, but they were not able to feed and develop. The cold apparently affected certain organs.

During October and November the cold-hardiness of the larvae increased very rapidly reaching a maximum hardness the first of December or very soon thereafter. They retained this maximum hardness through December, January, and February. During March they started to lose this cold-resistance, reaching their minimum cold-hardiness the first of May at which time their hardness was about equal to their hardness at mid-October. During October and the first half of November the cold-hardiness of larvae from the three hosts was similar, but during late November and early December the larvae from limber pine were the most hardy followed by lodgepole and ponderosa pine larvae. The order of hardness remained the same until May when the limber pine larvae became less hardy than those from the other two hosts.

The critical range of ponderosa pine larvae was from 10° to -1° in mid-October. By mid-December, when they reached maximum cold-hardiness, the range was -15° to -31° . They retained this

approximately 10° and that of limber pine larvae approximately 17° .

Cold-resistance tests of larvae from ponderosa pine from southern Utah, southern Colorado, northern Colorado, and Black Hills of South Dakota during January and February showed there was no difference in the hardiness of larvae from these rather distant localities.

In general the mortality produced during the winter months by exposures of 2 hours was approximately the same as exposures up to 24 hours. During the spring and fall when the larvae were active there was some additional mortality produced by longer exposures, particularly at temperatures in the upper part of the critical range.

Sudden changes of temperatures as contrasted with gradual temperature changes over a period of several hours produced no additional mortality.

The Black Hills beetle overwinters in the larval stage and is therefore the only stage subject to freezing temperatures in nature. Several tests made during the spring after the larvae had developed to the pupal and callow adult stages showed that the pupae are the most hardy followed by the larvae and adults. During June when the three stages were present, the critical range of the larvae from ponderosa pine was 10° to -5° . The pupae were 5° to $7\frac{1}{2}^{\circ}$ more cold-hardy and the adults approximately $2\frac{1}{2}^{\circ}$ to 5° less hardy than the larvae.

hardiness until soon after mid-March when they started to lose this maximum hardiness. By the first of May their resistance had decreased to a range of 11° to -8° . During May and June their hardiness decreased very little.

During the latter part of October the critical range of larvae from limber pine was from $12\frac{1}{2}^{\circ}$ to -5° , but soon after the first of December their critical range had changed to $-17\frac{1}{2}^{\circ}$ to -45° . The critical range remained constant through December, January, and February. Through March and April their resistance decreased, reaching a minimum degree of hardiness in May, at which time the critical range was 16° to $2\frac{1}{2}^{\circ}$.

The latter part of October the critical range of larvae from lodgepole pine was 5° to $-7\frac{1}{2}^{\circ}$, but by the first of December their critical range had dropped to -21° to -36° . Their critical range remained the same through December, January, and February. Through March and April their hardiness decreased and by the first of May the critical range was 10° to -5° . During May and June their hardiness decreased very little.

Conditioning infested logs at 36° for 18 days during January and February reduced the cold-hardiness of ponderosa pine larvae 7° and that of limber pine larvae about 15° below that of larvae in logs stored under natural temperature. Conditioning infested logs at 34° during February reduced the cold-hardiness of ponderosa pine larvae

Moisture in contact with the larvae inoculates the body fluids causing them to freeze at temperatures 3 to 5 degrees higher than dry larvae.

The male and female of the Black Hills beetle were equal in their cold-resistance.

During a drop of 40° in air temperature in 12 hours or a drop of $3\frac{1}{3}^{\circ}$ per hour the subcortical temperatures of ponderosa pine bark $\frac{7}{8}$ inch thick lagged approximately $3\frac{1}{2}$ hours, and the thinner $\frac{5}{16}$ lodgepole and $\frac{3}{8}$ inch ponderosa pine bark approximately $2\frac{3}{4}$ hours behind the air temperature. The difference in air temperature and subcortical temperature varied from 11° in the thicker bark to 7° in the thinner bark. With a drop of 30° in 6 hours or a drop of 5° per hour the lag in time was approximately the same as the $3\frac{1}{3}^{\circ}$ drop per hour; however, the difference between air and subcortical temperatures was greater. With the thicker bark the difference between air and subcortical temperatures was approximately 14.4° and the thinnest bark 8.6° . It is believed that under natural conditions the protection from cold amounts to 5 to 15° depending upon the thickness of bark, the rate of drop, and the amount of heat stored up in the tree.

An unseasonal low temperature of -15° registered on November 6, 1938 killed 29 percent of the brood on the Pike National Forest in Colorado. Larval mortality varied in the seven areas examined

from as low as 10 percent to as high as 40 percent. In general, mortality varied indirectly with bark thickness, the mortality under the thinner bark occasionally being as high as 100 percent and under bark of 1 inch or more in thickness practically no mortality occurred. The average of brood mortality on the south side of the trees was 38 percent and on the north side 26 percent. The bark on the average offered a protection of approximately 12° from outdoor temperature.

An examination of the infestation on the Roosevelt National Forest in April 1933 by Baumhofer revealed that some agent, presumably low temperature, had killed approximately 50 percent of the brood. If low temperature was responsible for this, it probably occurred on February 8, 1933 when a low of -34° was recorded.

A summary of minimum temperature records from official Weather Bureau stations applicable to the forests, where epidemics have occurred reveal that lethal low temperatures occur approximately 1 time in every 7 years in the ponderosa pine type. Lethal temperatures in limber and lodgepole pine types apparently occur less often. As a whole the Black Hills beetle is very well adapted to the minimum temperatures of its environment.

ACKNOWLEDGMENTS

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